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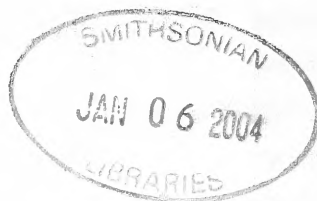


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### COVER IMAGE:

The California Academy of Sciences building on Market Street, San Francisco.  
(Left) This building, which opened to the public in 1891, faced on Market Street. It was one of two buildings built by the Academy on the Market Street property deeded to it by San Francisco business tycoon turned philanthropist and recluse, James Lick.  
(Right) The building that faced on Market Street was destroyed by the fire that engulfed much of the downtown area of San Francisco following the earthquake on 18 April 1906. The building seen to the left and behind the Market Street building housed the Academy's public museum and the research departments. The Market Street building, to which the museum building had been connected by an elevated bridge, or causeway, was leased by the Academy to various businesses to provide a steady stream of income to support its museum and other programs. (Images from the California Academy of Sciences Archives.)

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## The Genus *Roboastra* Bergh, 1877 (Nudibranchia: Polyceridae: Nembrothinae) in the Atlantic Ocean

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The systematics of the phanerobranch dorid genus *Roboastra* Bergh, 1877 in the Atlantic Ocean is reviewed. *Roboastra europaea* García-Gómez, 1985 is redescribed and its geographical range updated. *Roboastra caboverdensis* sp. nov. is described from material from Cape Verde Archipelago. The two species differ in their color pattern. The arrangement of the yellow lines or bands differs between the two species with denser lines in *R. europaea*. The base of the rachidian radular tooth is more curved in *R. caboverdensis* than in *R. europaea* and the upper cusp of the inner lateral tooth is bifid in *R. europaea* while in *R. caboverdensis* it is simple.

Se revisa la sistemática del género del dórido fanerobránquio *Roboastra* Bergh, 1877 en el Océano Atlántico. Se redescrive *Roboastra europaea* García-Gómez, 1985, así como se actualiza su distribución geográfica. Se describe *Roboastra caboverdensis* sp. nov. a partir de material procedente del archipiélago de Cabo Verde. Las dos especies se diferencian por su patrón cromático. La disposición de las líneas o bandas amarillas difiere entre las dos especies, con un mayor número de ellas en *R. europaea*. La base del diente radular raquídeo está más curvada en *R. caboverdensis* y la cúspide superior del diente lateral interno es bífida en *R. europaea* mientras que en *R. caboverdensis* es simple.

The genus *Roboastra* was described by Bergh (1877). Until Burn's revision (1967), this genus included three species: *Roboastra gracilis* (Bergh, 1877) (type species), *R. rubropapulosa* (Bergh, 1905) and *R. luteolineata* (Baba, 1936), all with an Indo-Pacific distribution. Burn described a new species, *R. arika* and suggested that *R. rubropapulosa* should be considered as a synonym of *R. gracilis*. Some years later, Farmer (1978) described *R. tigris* from the eastern Pacific. García-Gómez (1985) then described *R. europaea* from the Strait of Gibraltar, the only species known from Atlantic-Mediterranean waters. Thus, to date, the genus *Roboastra* includes five named species. The only morphological data stem from the original descriptions, with the exception of the redescription of *R. gracilis* by Burn (*op. cit.*) and its taxonomic comparison with *R. luteolineata* by Hamatani and Baba (1976).

No additional studies have treated members of this genus except for that of *R. tigris* (Carté and Faulkner 1983, 1986) and, more recently, in which *R. europaea* was the focus of molecular phylogenetic (Grande *et al.*, 2002) and feeding ecology (Megina and Cervera 2003) studies. Recent collections from the Cape Verde Archipelago (West Africa) have yielded several specimens of a second undescribed Atlantic species of this genus.

In this paper, we describe the new species from Cape Verde. We also redescribe *R. europaea*, largely from material from the Iberian Peninsula, and update its geographical range.

### MATERIAL AND METHODS

Specimens were dissected by dorsal incision. At least three specimens of each species were examined anatomically. Their internal features were examined and drawn under a dissecting microscope with a camera lucida. Particularly interesting soft parts were critical-point dried for scanning electron microscopy (SEM). Special attention was paid to the morphology of the reproductive system. The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination by scanning electron microscopy.

The materials examined are deposited in the California Academy of Sciences, San Francisco (CASIZ), the Museo Nacional de Ciencias Naturales, Madrid (MNCN) and the Museu Municipal de Funchal (Historia Natural) (MMF).

### SPECIES DESCRIPTIONS

#### Family Polyceridae Alder and Hancock, 1845

#### Subfamily Nembrothinae Burn, 1967

#### Genus *Roboastra* Bergh, 1877

#### *Roboastra europaea* García-Gómez, 1985

(Figs. 1A, 2, 3A–C, 4, 5, 6)

**MATERIAL EXAMINED.**—MNCN 15.05/46612. 1 specimen, 10 m depth, Torre, Marbella, Spain, July 1995, J.L. González, 30 mm. CASIZ 166049. 1 specimen, 10 m depth, Torre, Marbella, Spain, September 1995, M.T.Barrea, 18 mm. CASIZ 166053. 2 specimen, Torre, Marbella, Spain, August 1996, K.L. Schick, 10.7m, 15 y 19 mm. MNCN 15.05/29203, 1 specimen, La Herradura, Granada, Spain, February 1993, A.Barrajón and M. Zarauz, 14 mm. MMF 31021, 1 specimen, 100 m depth, Funchal, Madeira, June 1999, 35 mm. MNCN 15.05/46613. 1 specimen, 20 m depth, Ponta de Baleeira, Sagres, Portugal, July 2002, M.Pola, 14 mm. MNCN 15.05/46613. 1 specimen, 20 m depth, Ponta de Baleeira, Sagres, Portugal, July 2002, M.A. Malaquias, 10 mm. Specimens were collected on rocks and were measured preserved.

**DISTRIBUTION.**—This species is known mainly from the Strait of Gibraltar and southern Iberian Peninsula (García-Gómez 1985; 2002<sup>1</sup>; Cervera et al. 1988; García-Gómez et al. 1989, 1991; Moreno and Templado 1998; Schick 1998; Megina 2000; Ocaña et al. 2000; Sánchez-Tocino et al. 2000; Grande et al. 2002; Megina and Cervera 2003). One misidentified specimen of *Placamopherus* from Madeira deposited at the Natural History Museum (London) (Reg. No. 1863.9.19.3), supposedly collected by Rev. R. Lowe, was correctly identified as belonging to *Roboastra*, very probably *R. europaea*. This conclusion has been strongly supported by the recent collection of one specimen (also photographed) of this species at Funchal Harbour.

This species has been also recorded in southwestern Portugal (Calado et al. 2002) and Catalanian coasts (northeastern Iberian Peninsula, Mediterranean Sea) (K.L. Schick, pers. commun.).

<sup>1</sup> The specimens described by García-Gómez (2002) are the same of those described by this author in 1985 for the original description of this species.



**EXTERNAL MORPHOLOGY** (Fig. 1A).— The body is elongate and limaciform. The preserved animals are 10–40 mm in length. The body surface is lightly uneven with the edge of the mantle not sharply angled. Foot is linear with a pointed posterior end of the foot. The head is rounded with a pair of perfoliate rhinophores (bearing 30–35 lamellae) that are completely retractile into their sheaths. The oral tentacles are well developed and grooved dorsolaterally along a part of their

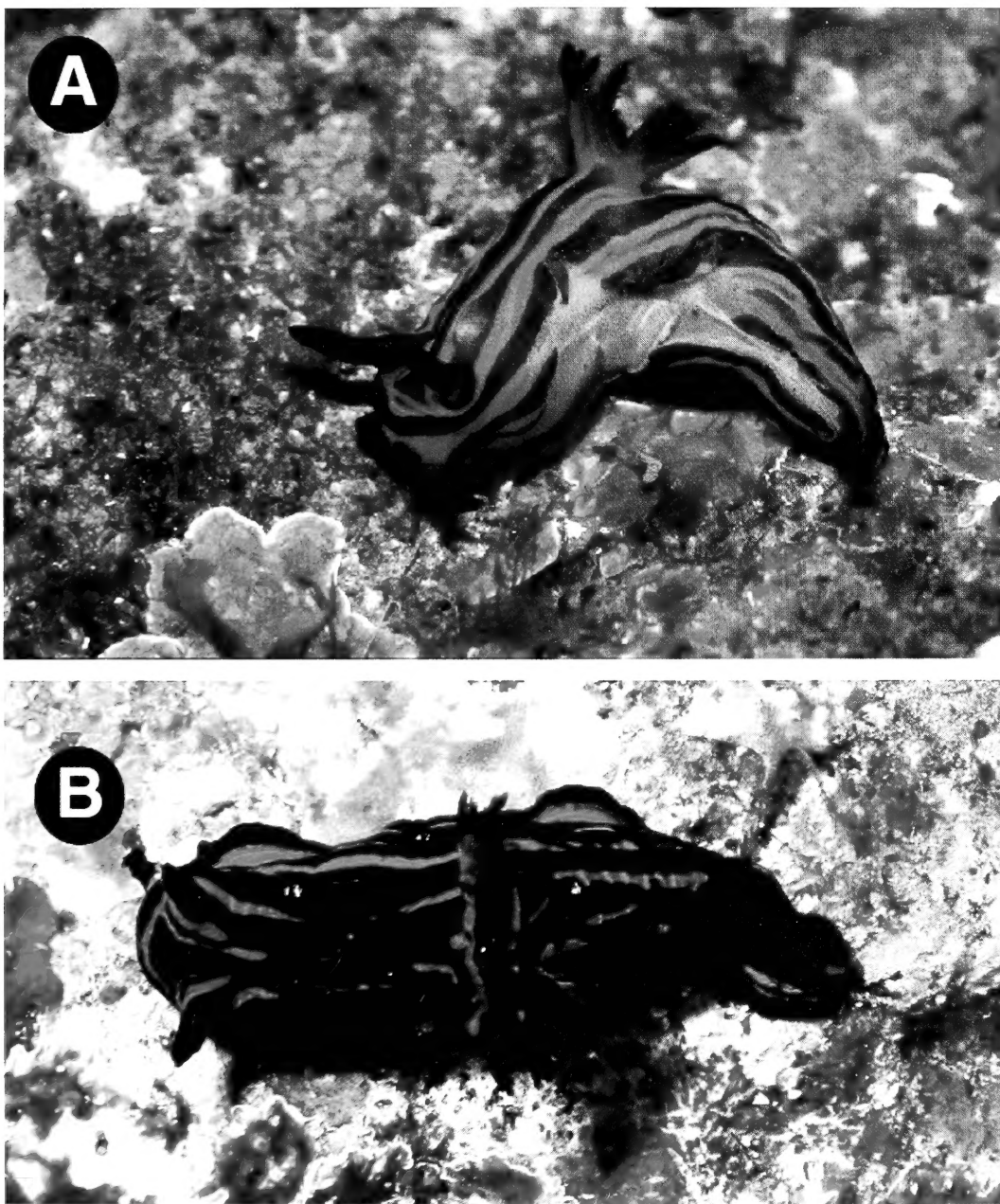


FIGURE 1. Living animals. A. *Roboastrea europaea* García-Gómez, 1985, specimen from Ponta da Baleeira, Sagres, Portugal. B. *Roboastrea caboverdensis* sp. nov., specimen from Banco Joao Valente, Ilha da Boavista, Cape Verde.

length. There are five non-retractile, bipinnate gills surrounding the anal papilla and forming a half circle; the three central gills are larger than the two lateral ones. The genital aperture is located midway between the gills and rhinophores, on the right side. The body wall is highly muscular. Regarding the color pattern, this species can exhibit two color phases. One of them has a grey or bluish grey ground color; the other has dark blue ground color. Both phases have several yellow or yellowish orange bands on the notum and both sides of the body. These bands are variable in number, shape, length and width. The rhinophores and oral tentacles are grey/bluish grey to dark blue. The inner side of the gill rachis are yellow or yellowish orange. The outer side is frequently also this color, but rarely may be a dark blue. The secondary pinnae are grey/bluish grey to dark blue. The yellow/ yellowish orange areas are surrounded by a tiny violet line that is easily visible in most animals, except in the darkest individuals. The rhinophoral sheaths are also grey/bluish grey to dark blue (Fig. 1A).

**INTERNAL MORPHOLOGY.**— A general view of the internal anatomy can be seen in Figure 2. The buccal mass is elongate and tubular, well developed with a pair of elongate pouches opening into the digestive system at the junction of the oral tube and muscular pharynx (Fig. 3). The salivary glands are short and thick, entering on the buccal mass and flanking the esophagus. The labial cuticle lacks any armature. There is a well developed blood gland that is granular in texture. The radular formula of two specimens of 15 mm length (preserved) is  $23 \times 4.1.1.1.4$ , and that of the 30 mm specimen (preserved) has the formula  $25 \times 4.1.1.1.4$ . (Fig. 4A–C). The rachidian tooth (Fig. 4B) is broad, thin and curved at its base with three well-differentiated cusps. The inner lateral tooth

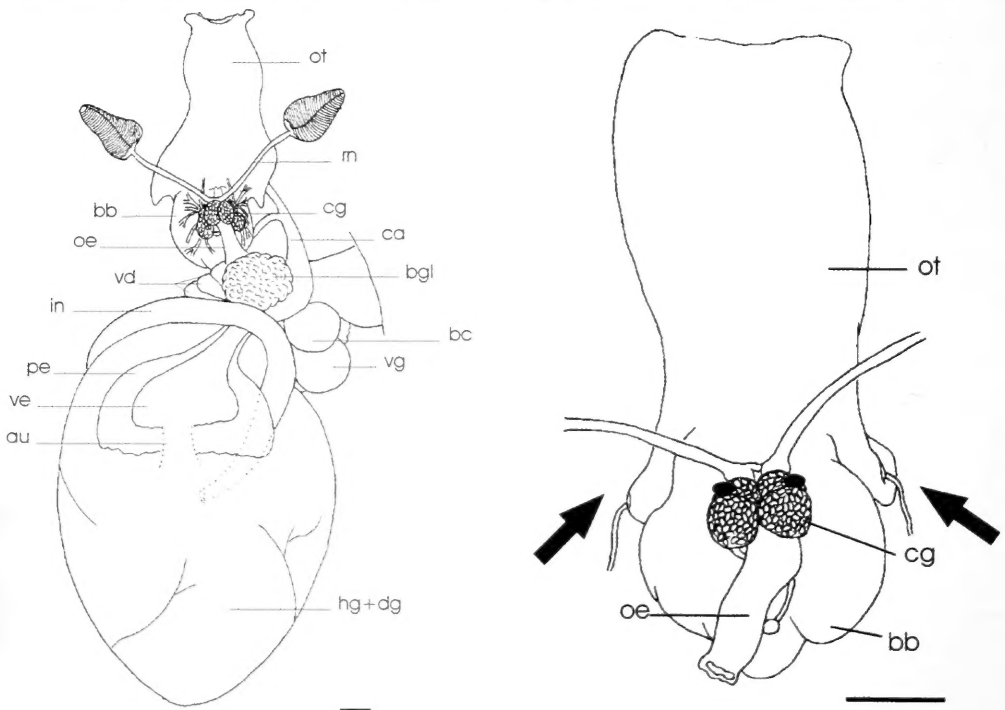


Figure 2 (left). *Roboastra europaea* García-Gómez, 1985. General arrangement of the internal organs, au = auricle, bb = buccal bulb, bc = bursa copulatrix, bgl = blood gland, ca = cephalic artery, cg = cerebral ganglion, hg+dg = hermaphrodite gland+digestive gland, in = intestine, oe = oesophagus, ot = oral tube, pe = pericardium, rn = rhinophoral nerves, vd = vas deferens, ve = ventricle, vg = vestibular gland.

FIGURE 3 (right). *Roboastra europaea* García-Gómez, 1985. Detail of the oral tube and buccal mass.

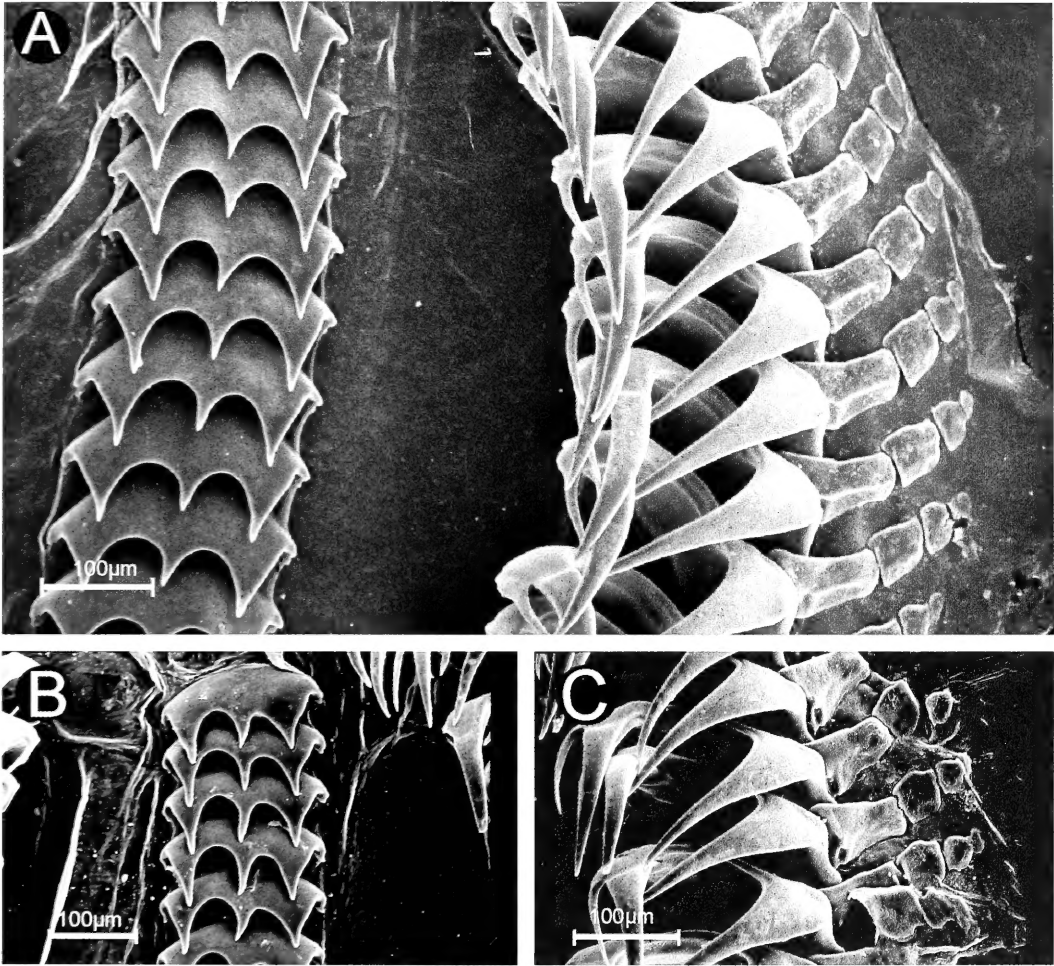


FIGURE 4. *Roboastrea europaea* García-Gómez, 1985. CASIZ 166053, scanning electron micrographs of radula: A. Half-row of radular teeth. B. Rachidian teeth. C. Inner lateral tooth.

(Fig. 4C) has a strongly curved bifid inner cusp. The inner branch of this cusp is thin and smaller than the second. The outer cusp is undivided with a long spur-like denticle near the base. The remaining lateral radular teeth are quadrangular and lack cusps or denticulation and become smaller near the margin.

**REPRODUCTIVE SYSTEM** (Fig. 5).— The hermaphroditic duct widens into a S-shaped ampulla which has thick walls. The bursa copulatrix is rounded and larger than the seminal receptacle, which is elongate. The seminal receptacle has a short duct that connects to the vagina near the bursa. The deferent duct, which lacks a morphologically well-differentiated prostate, is long and coiled and ends in a dilated penial atrium. The vestibular gland is large with muscular walls, convex on one side and concave on the other. The penis is located within the distal end of this muscular portion, and it is armed with, at least, three different kinds of hooked and chitinous spines arranged in helicoidal rows. The types of spines and their arrangement on the penis are shown in Figure 6.

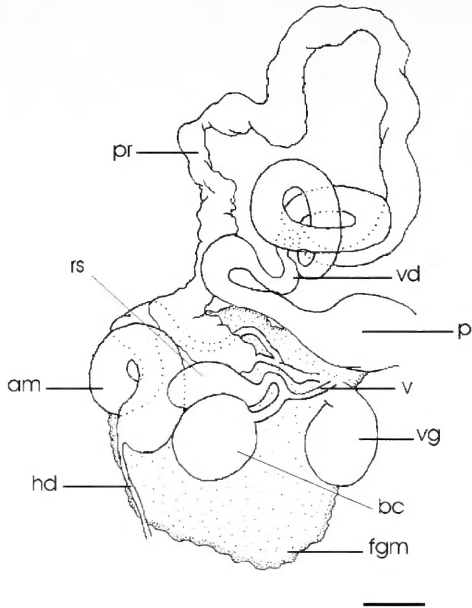


FIGURE 5. *Roboastra europaea* García-Gómez, 1985. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, hd = hermaphrodite duct, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, vg = vestibular gland.

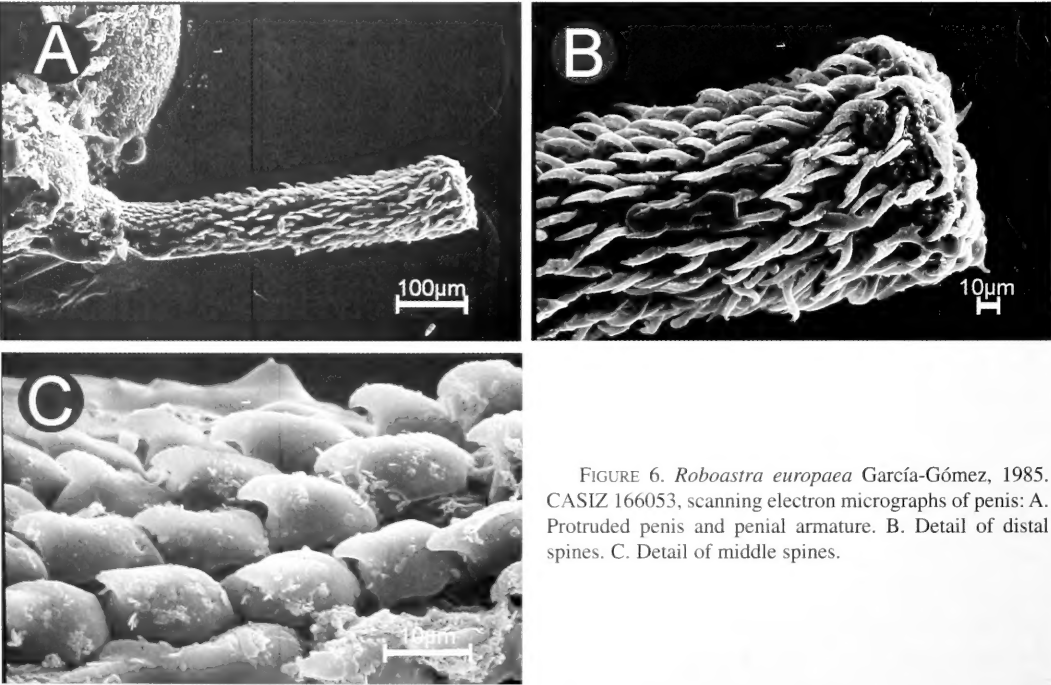


FIGURE 6. *Roboastra europaea* García-Gómez, 1985. CASIZ 166053, scanning electron micrographs of penis: A. Protruded penis and penial armature. B. Detail of distal spines. C. Detail of middle spines.

***Roboastrea caboverdensis* Pola, Cervera, and Gosliner, sp.nov.**

(Figs. 1B, 7, 8, 9A–C, 10, 11A–D)

**TYPE MATERIAL.**— HOLOTYPE: CASIZ 166047, 1 specimen, 38 m depth, 15 miles NW Santo Antao Island, Cape Verde Archipelago, July 2002. PARATYPES: MMF35083, 1 specimen, Tarrafal Island, Cape Verde Archipelago, December 1998, P. Wirtz, 25 mm. MNCN. 15.05/46614, 2 specimen, 20 m depth, Banco Joao Valente, Boavista Island, Cape Verde Archipelago, August 2002, M.A. Malaquias, 26/30 mm (70 mm in life). CASIZ 166052, 2 specimen, 30 m depth, Banco Joao Valente, Boavista Island, Cape Verde, August 2002, M.A. Malaquias, 31/37 mm (70 mm in life). MNCN. 15.05/46617. 3 specimens, Boavista Island, August 2002, C. Grande, 13/15/18 mm. CASIZ 166050, 1 specimen, Sao Vicente, October 2002, G. Calado, 20mm. Specimens were collected on rocks and were measured preserved.

**ETYMOLOGY.**— The name *caboverdensis* refers to the Cape Verde Archipelago where this species is found.

**DISTRIBUTION.**— Thus far, known only from Cape Verde Archipelago.

**EXTERNAL MORPHOLOGY.**— The body is elongate and limaciform with a long and pointed posterior end of the foot. The preserved animals are 10–40 mm in length. The living animals (Fig. 1B) may reach 70 mm in length. The body surface is strongly wrinkled. The foot is linear. The head is rounded with a pair of conical, completely retractile, perfoliate rhinophores with approximately 35 tightly packed lamellae. The oral tentacles are strongly developed and dorsolaterally grooved along a part of their length. There are five non-retractile tripinnate gills, with the three anteriormost being more highly developed. The gills form a semicircle surrounding the anal papilla. The genital pore opens on the right side, midway between the gills and rhinophores. The ground color is dark blue, almost black. A wide yellow submarginal band follows the inner notal edge. This band is interrupted in some specimens. A second yellow band arises from the former, just in front of both rhinophores and surrounds the inner side of their sheaths, continuing to the rear to the base of the gills. These bands can bifurcate at their origin. In this case, the sheath of the rhinophores is surrounded by the shorter branch. In either situation, these bands surround the gill to join each other posteriorly. These last bands can be interrupted or continuous. The edge of foot is also bordered by a wide yellow band. On the sides of the body, just below the notal edge, there is a line of the same colour that bifurcates and surrounds the genital pore, continuing to the end of the posterior end of the foot. Both branches can be continuous or not. Moreover, several yellow lines, varying in number and length, are arranged between the dorsal and the foot bands. The oral tentacles, the rhinophores and the posterior part of their sheath are also blue-black. The gills are blue-black, but the inner and outer sides of the rachis of each one have a yellow line between them.

**INTERNAL MORPHOLOGY.**— The general arrangement of the internal organs is shown in Figure 7. The anterior digestive tract begins with a long thick-walled muscular oral tube, that continues into the buccal mass. At their junction, a pair of elongate pouches open into the digestive system (Fig. 8). There is a pair of small, short and wide salivary glands on the buccal mass, flanking the esophagus. The radular formula of two specimens of 70 mm (in life) is  $33 \times 3-4.1.1.1.3-4$  (Figs. 9A–C). The rachidian tooth (Fig. 9B) is broad, clearly curved at the base, having three well-differentiated cusps. The inner lateral tooth (Fig. 9C) is hooked with two well developed elongate cusps. The inner one is very long, having sharp and curved edges on the internal side and a prominent projection (see the arrows Fig. 9A) on its outer edge. The outer lateral teeth (3 to 4) are smaller and quadrangular without prongs, and decreasing in size from the inner to the outer side of the radula. A labial cuticle is present, but lacks armature.

**REPRODUCTIVE SYSTEM.**— The reproductive system is shown in Figure 10. The hermaphro-

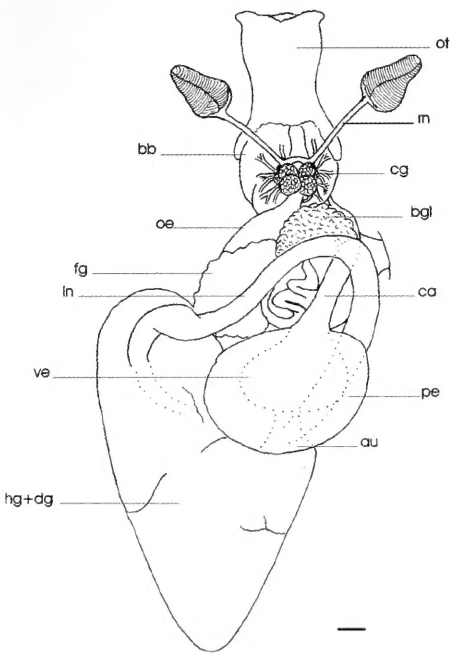


FIGURE 7. *Roboastra caboverdensis* sp. nov. General arrangement of the internal organs. au = auricle, bb = buccal bulb, bgl = blood gland, ca = cephalic artery, cg = cerebral ganglion, fm = female gland, hg+dg = hermaphrodite gland+digestive gland, in = intestine, oe = oesophagus, ot = oral tube, pe = pericardium, rn = rhinophoral nerves, ve = ventricle.

with, at least, three different kind of spines arranged in helicoidal rows. Types of spines and their arrangement on the penis are shown in Figures 11A–D. The bursa copulatrix is rounded and the seminal receptacle elongate. The seminal receptacle joins with the vagina, near the bursa via a short duct. The vagina is short and straight, opening into the genital atrium, near the vestibular gland. This gland is very well developed, flattened, with muscular walls.

## DISCUSSION

In 1985, García-Gómez described the first species of the genus *Roboastra* in the Atlantic Ocean, from the Strait of Gibraltar. The original description of the external anatomy, radula and reproductive system of *Roboastra europaea* is in agreement with our specimens of this species; however, our specimens exhibit a different pattern of coloration than has been previously described for this species (Schick 1998; Megina 2000; García-Gómez 2002:224, phot. 44<sup>2</sup>; Sanchez 2001). Moreover, it is confirmed that the spicules of the surface of the mantle mentioned in the original description do not exist (perhaps they were an artifact of preservation). A pair of small, short and wide salivary glands on the buccal mass flanking the esophagus are described for the first time. These salivary glands are present in the other two genera of the subfamily Nembrothinae,

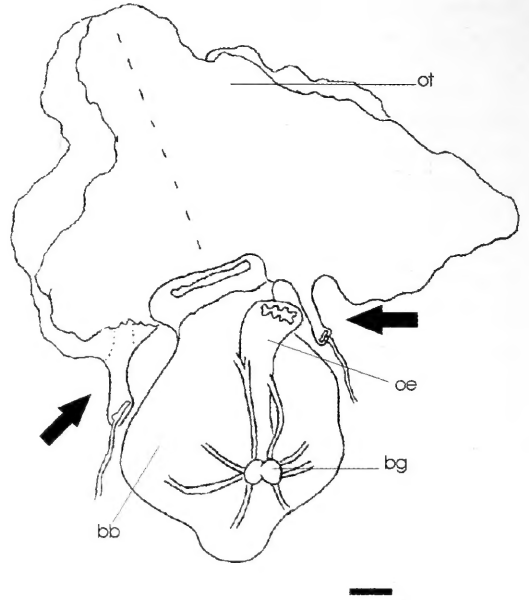


Figure 8. *Roboastra caboverdensis* sp. nov. Details of the oral tube and buccal mass, bb = buccal bulb, bg = buccal ganglion, oe = oesophagus, ot = oral tube.

ditic duct has an “S” shaped ampulla that continues into the spermoviduct. The vas deferens is long and coiled, with a uniform width. It is slightly narrower in the prostatic part. It ends in a dilated penial section. The penis is armed

<sup>2</sup> The colour pattern supplied by García-Gómez (2002) is an adaptation from his original description (García-Gómez, 1985), with additional and later information, although the specimens included in the “Material” section are the same in both references.



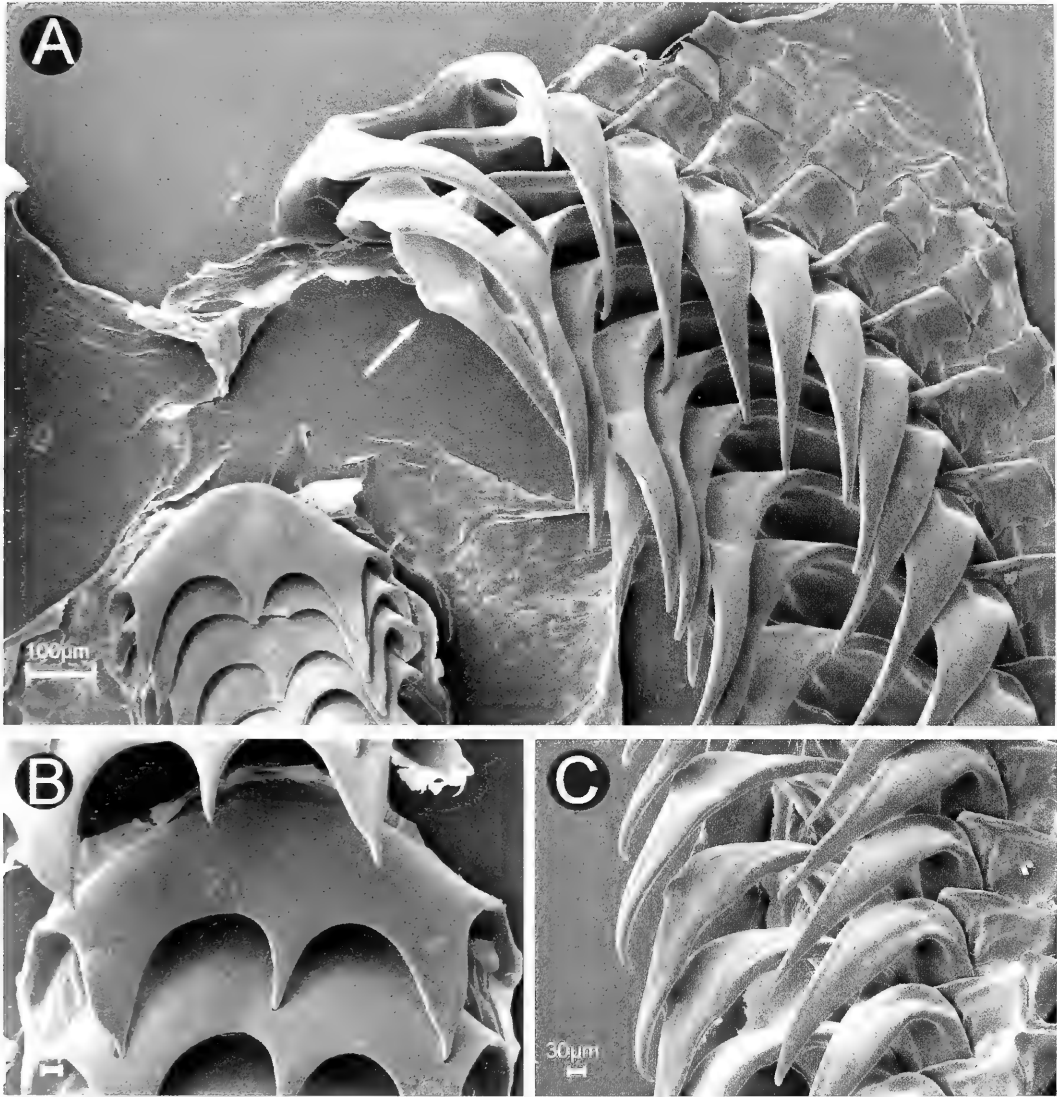


FIGURE 9. *Roboastrea caboverdensis* sp. nov. CASIZ 166052, scanning electron micrographs of radula. A. Half-row of radular teeth. B. Rachidian teeth. C. Inner lateral tooth.

*Nembrotha* and *Tambja*, but in these they are longer and more robust than in *Roboastrea*. García-Gómez (1985) did not describe the presence of a pair of elongate pouches that open into the digestive system at the junction of the oral tube and muscular pharynx. The function of these structures is still unknown; nevertheless, Burn (1967) described similar structures in *Roboastrea gracilis*.

The external and internal features of *Roboastrea caboverdensis* permit us to distinguish it from its congeneric Atlantic species. The arrangement of the yellow lines or bands in both species is different and are more numerous and tightly packed in *R. europaea*. Moreover, *R. europaea* has two colour phases, light and dark (see Cervera et al. 1988 and Ocaña et al. 2000, for a colour picture of the light phase).

Regarding the internal anatomy of both species, the base of the rachidian radular tooth is more

curved in *R. caboverdensis* and the upper cusp of the inner lateral radular tooth is bifid in *R. europaea* while in *R. caboverdensis* it is simple. The reproductive system of *R. caboverdensis* is similar to that described for *R. europaea* except that the portion of the ejaculatory duct near the prostate is more highly convoluted in *R. europaea*. The penis in both cases is armed and the spines, of three different sizes and shapes, are implanted in heli-coidal rows. In both *R. europaea* and *R. caboverdensis*, the distal two-thirds of the penis has elongate, curved spines, and the basal spines are medium sized but straighter than the distal ones. Between them, there are some rows of short, curved spines, a few with little spines just behind them.

There is another dark blue/black with yellow bands or lines nembrothid in the Cape Verde Archipelago, *Tambja simplex* Ortea and Moro, 1998. However, the yellow pattern of this species has few lines with a different arrangement, and the internal anatomy (salivary glands, labial cuticle, radular teeth and reproductive system) are characteristic of *Tambja* (Ortea and Moro 1998; Cervera et al. 2000).

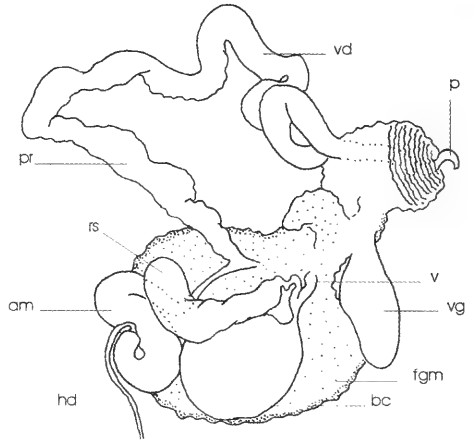


FIGURE 10. *Roboastra caboverdensis* sp. nov. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, hd = hermaphrodite duct, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, vg = vestibular gland.

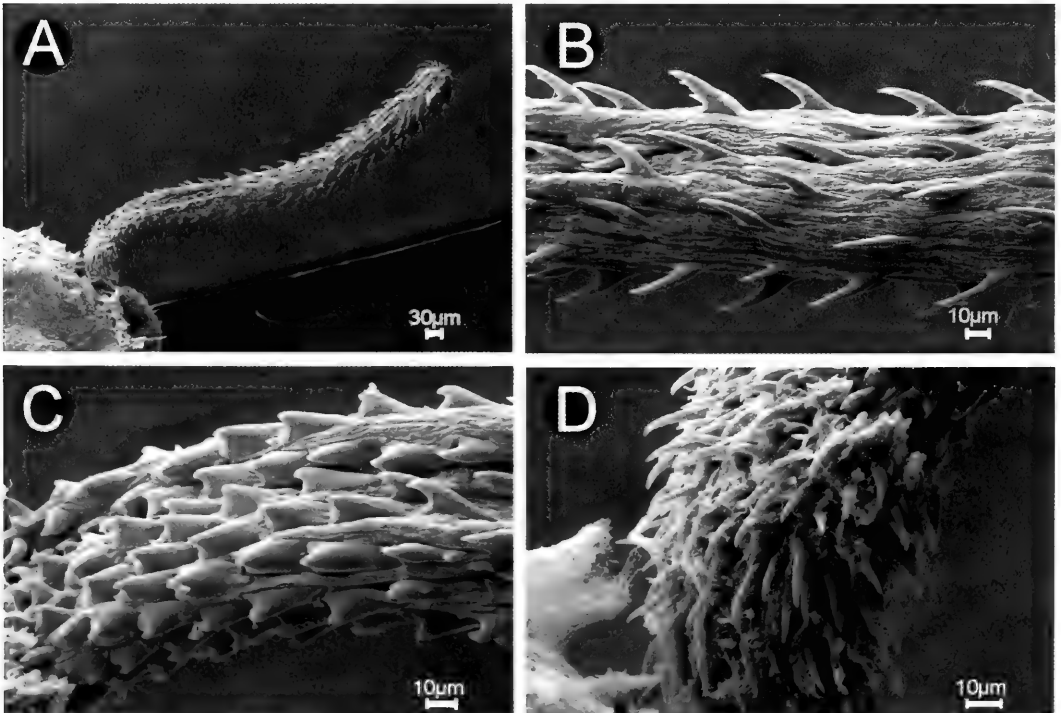


FIGURE 11. *Roboastra caboverdensis* sp. nov. MNCN 15.05/46614. A. Protruded penis. B. Detail of distal spines. C. Detail of middle spines. D. Detail of basal spines.



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## Redescription of *Halgerda graphica* Basedow and Hedley, 1905, with Observations on External Morphological Variation within Selected Species of *Halgerda* (Mollusca: Nudibranchia)

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*Halgerda graphica* Basedow and Hedley, 1905 is redescribed based on examination of two specimens; one collected in 1904 from Middle Harbour, Sydney, Australia, housed at the Australian Museum, Sydney, and another specimen collected in 1990, from Port Moorowie, near the type locality (Kangaroo Island, South Australia). The reproductive system is described and illustrated for the first time. This species has frequently been misidentified due to having similar external morphology to other *Halgerda* species. A comparison is made to those species. *Halgerda graphica* has a unique combination of external and internal characters that confirm it as a distinct *Halgerda* species. The external characters include a “hieroglyphic” pattern of yellow and black markings on the notum, small, similar-size dark spots on the ventral surface, a small, sparse, dark-colored gill and rhinophores with a white base, dark tip and a dark line on the posterior side. The external color variations of *Halgerda dichromis* Fahey and Gosliner, 1999, *H. okinawa* Carlson and Hoff, 2000 and *H. willei* Eliot, 1904 are also described, illustrated and compared to externally similar species. It is the unique combination of external morphological characters such as the color and pattern on the notum, the structure and color of the gills and rhinophores that help to distinguish each species, although examination of internal morphology can confirm the identification.

Basedow and Hedley (1905) described the nudibranch *Halgerda graphica* from two specimens dredged off Antechamber Bay, Kangaroo Island, South Australia. They had at the time examined a third specimen, which, although not included in the original description, they indicated that it belonged to their new species. The original description of the external and radular morphologies of the specimens were quite detailed, but the authors did not provide a description of the reproductive morphology. This species did not show up again until 1990. In the meantime, other authors (e.g., Coleman 1975, 2001; Kay 1979; Kay and Young 1969; Wells and Bryce 1993) have erroneously attributed the name *Halgerda graphica* to other species.

The present study describes two additional specimens of *Halgerda graphica*; the single specimen mentioned by Basedow and Hedley, collected in approximately 1904 at Middle Harbour, Sydney, and an additional specimen collected by N. Holmes in 1990 from Port Moorowie, Yorke Peninsula, South Australia.

The nudibranch genus *Halgerda* Bergh, 1880 has been studied extensively in recent years (Rudman 1978; Willan and Brodie 1989; Carlson and Hoff 1993, 2000; Gosliner and Fahey 1998;

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Fahey and Gosliner 1999a, 1999b, 2000, 2001a, 2001b). Since 1998, the number of described species increased from 14 to 35. Among *Halgerda* species are several that display external color variation in specimens from similar habitats and from varying geographic ranges. Four species, in particular, seem to be most commonly confused: *Halgerda graphica*, *H. willeyi*, *H. okinawa* Carlson and Hoff, 2000, and *H. dichromis* Fahey and Gosliner, 1999. The present study illustrates the color variations that can cause misidentification of these four species in the field and then makes comparisons with the externally most similar species. Field notes and photographic records of many observers, both amateur and professional, provide the basis of the discussion on external color variation presented in this paper.

#### DESCRIPTIONS OF TAXA

##### **Labiostomata Valdés, 2002**

##### **Family Discodorididae Bergh, 1891**

##### **Genus *Halgerda* Basedow and Hedley, 1905**

(Type species: *Halgerda formosa* Bergh, 1880, by monotypy)

##### ***Halgerda graphica* Basedow and Hedley, 1905**

(Figs 1–3)

**TYPE MATERIAL.**— The type material is probably lost; it is not at the Australian Museum. The type locality is Kangaroo Island, South Australia. The authors (Basedow and Hedley 1905) mention an additional specimen deposited at the Australian Museum, Sydney (C18168, Location #016276, collector not named) from Middle Harbour near Sydney, in September 1904. This specimen was examined and is both described below and hereby designated as the neotype.

**OTHER MATERIAL EXAMINED.**— South Australian Museum, TD16542, one specimen, dissected, Port Moorowie, Yorke Peninsula, South Australia. 10 m deep, collected by Nigel Holmes, 15 December 1990.

**EXTERNAL MORPHOLOGY.**— Because there are no photographs or drawings available for specimen C18168 (1904), the following is a description of the specimen collected in 1990 by N. Holmes. This specimen is nearly identical to the drawing and description of *Halgerda graphica* provided by Basedow and Hedley in 1905 (Fig. 1A).

The preserved animal is 28 mm in length. The body profile is rounded, convex (Fig. 1B) and the dorsum has a low-ridged pattern. There are no small marginal tubercles. There is a low central ridge running the length of the dorsum that splits into several smaller ridges as it nears the gill pocket. The ridges have orange-yellow crests. The background color of the dorsum is gray-white. Between the ridges are black spots with some spots circled or semi-circled with the same yellow color as the ridges. The dark spots closest to the mantle edge are smaller than those on the dorsum. The mantle margin is translucent white when viewed dorsally, but when viewed ventrally, a yellow margin is apparent. On the underside of the mantle and along the side of the foot are dark spots of various sizes. The foot margin is yellow (Fig. 1C). The oral tentacles are long and tapered.

The long rhinophores have a bulging club that is tapered at the tips. The club is angled posteriorly and there is dark brown to black coloration around the top half of the club up to the tip. The base is translucent white and there is a dark line on the posterior side of the rhinophores that extends from the base to the tip.

The bipinnate gill lies flat over the dorsum and is moderately pinnate. Each of the four main gill rachae has a brown stripe on the anterior sides. The anal papilla is long and is the same color as the body.

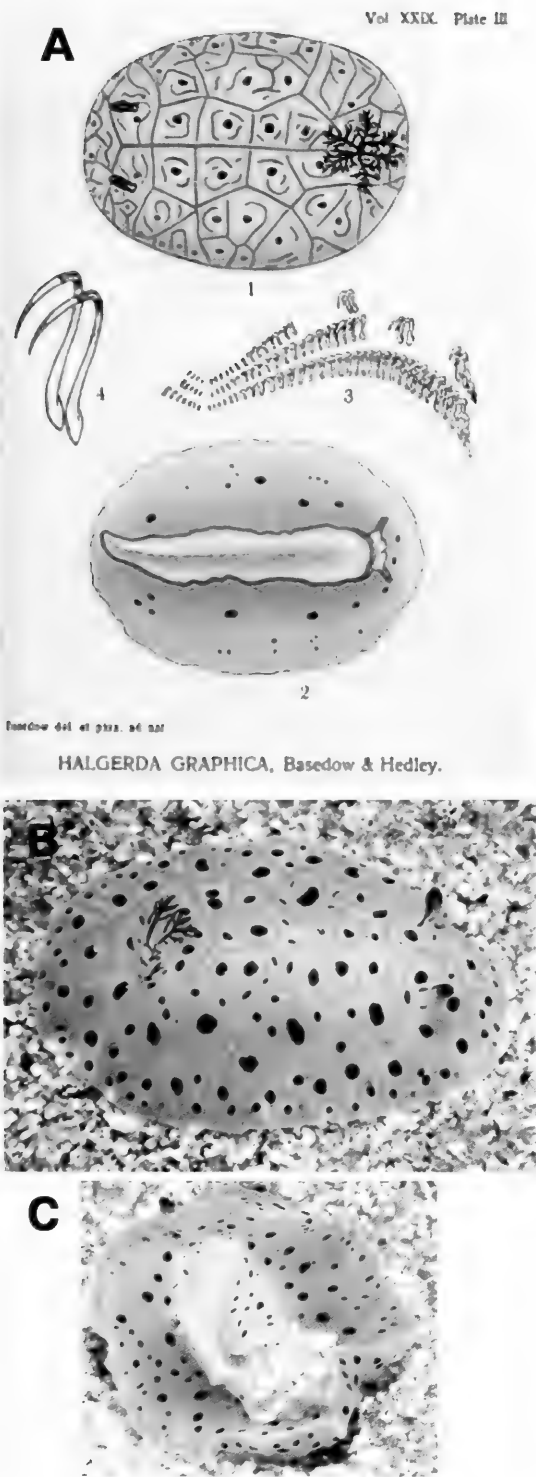


FIGURE 1. A. *Halgerda grafica* Basedow and Hedley, 1905, from the original color plate. B. *Halgerda grafica* South Australian Museum, (TD16542), photographed and collected by N. Holmes, 1990. Dorsal view. C. Ventral view.

**BUCCAL ARMATURE.**—The buccal mass has dark spots. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the specimen collected in 1990 is: 43x30.0.30 (TD16542) (Fig. 2A). The radular formula of the specimen collected in 1904 could not be determined due to poor preservation and deterioration of the radula. The three outer teeth are much smaller than the inner and middle lateral teeth and the outer two teeth have tiny denticles (Fig. 2B). The 8 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 2C) and are arranged in a shallow V-shaped pattern in the center of the radula. The middle lateral teeth are hamate (Fig. 2D) with long, pointed hooks. They have a flattened flange, which overlaps the adjacent tooth.

**REPRODUCTIVE SYSTEM.**—The reproductive system is triaulic (Fig. 3). The long ampulla is tubular, curved into a complete loop and protrudes away from the bursa and prostate. The ampulla narrows into the post-ampullary duct, which bifurcates into the vas deferens and oviduct. The long oviduct enters the female gland mass. The female gland mass is about the same size as the bursa copulatrix. The long vas deferens separates from the ampulla and widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well differentiated as in most other members of *Halgerda*. The muscular portion of the deferent duct leaves the distal prostate in a long duct that curves into one loop and multiple half-loops, then enters the wide penial bulb. The long uterine duct emerges from the female gland mass and joins the ovoid receptaculum seminis near its base. The duct con-

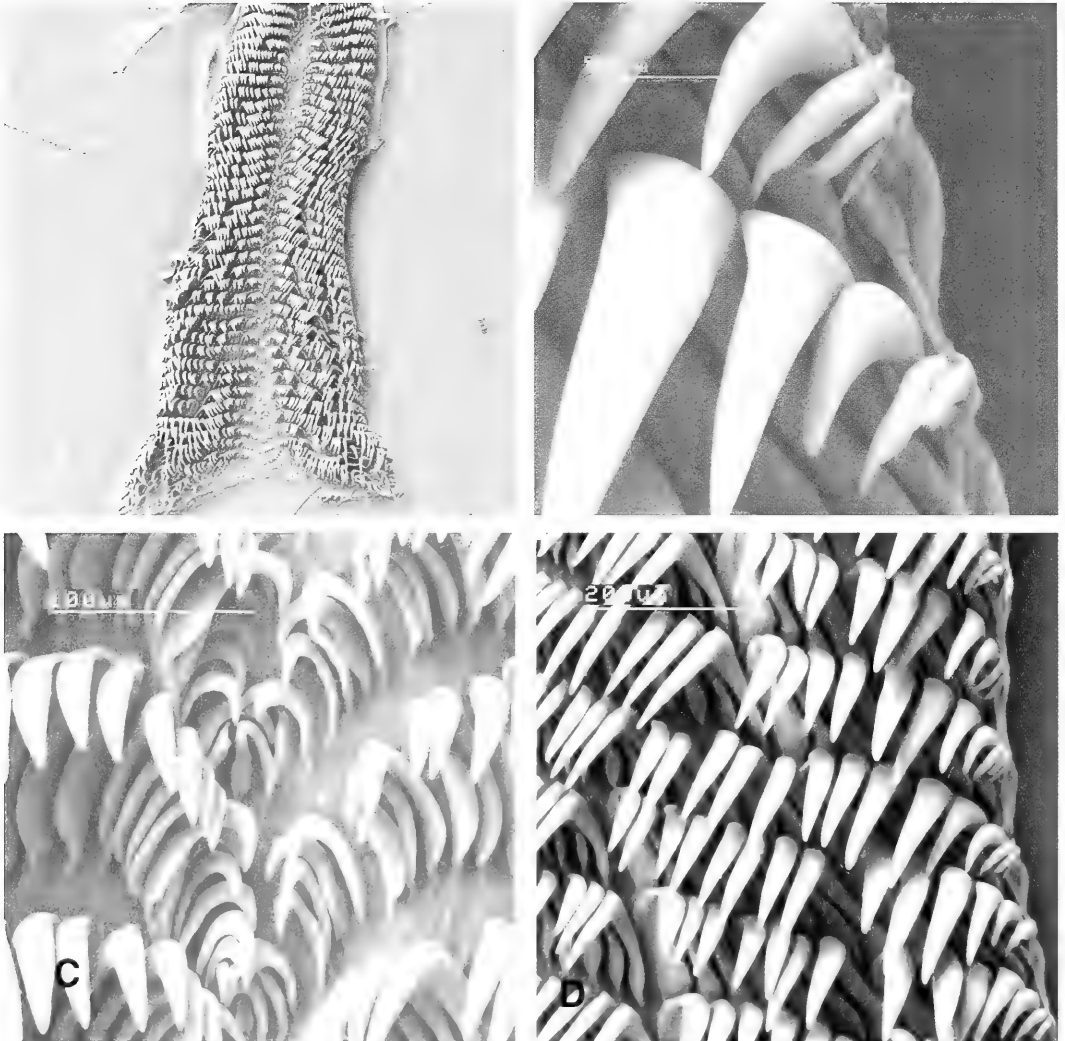


FIGURE 2. Radular morphology of *Halgerda grafica* (TD16542). A. Entire radula. Scale = 2 µm. B. Outer lateral teeth. Scale = 50 µm. C. Inner lateral teeth. Scale = 100 µm. D. Middle lateral teeth. Scale = 20 µm.

necting the receptaculum and the bursa is long and coiled. The receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. It lies under the bursa, but is not embedded in the prostate. The prostate does not completely cover the bursa copulatrix as is common in other, more highly derived species of *Halgerda*, but lies in a thin layer over two-thirds of the bursa. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit into the bulbous vagina that is adjacent to the base of the penial sheath, is a muscular sphincter. The vagina has long folds in the walls and tubercular glands on the exterior. The common genital aperture is wide, large and has long fleshy folds that extend through the body wall. The opening of the female gland mass is adjacent to the genital aperture.

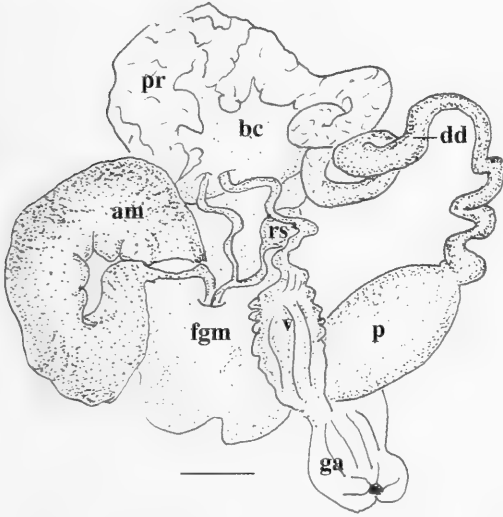


FIGURE 3. Reproductive morphology of *Halgerda grafica*. Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.25 mm.

convoluted deferent duct, a bulbous penial sheath and a wide, muscular vagina. Radular characters also have similarities to other *Halgerda* species. Those characters are hooked mid-lateral teeth, finely denticulate outer teeth that are much smaller than the remaining teeth, and small inner lateral teeth.

Because of the similarity in external coloration of *Halgerda grafica* to *H. gunnessi* Fahey and Gosliner, 2001, *H. johnsonorum* Carlson and Hoff, 2000 and *H. willeyi* Eliot, 1904, these three are herein compared and contrasted to *H. grafica*. However, because Carlson and Hoff (2000) have already compared *H. grafica* to *H. okinawa*, we will not repeat what they have already done. Neither will we repeat what Fahey and Gosliner said when they compared *H. gunnessi* to *H. johnsonorum* and to *H. formosa* Bergh, 1880, nor what Carlson and Hoff (2000) had to say when they compared *H. johnsonorum* to *H. willeyi*. Rather, we encourage reference to their respective papers. Here we concentrate on comparing the external morphology of *Halgerda grafica* to its most similar species.

All four species of greatest concern to us, *Halgerda grafica*, *H. gunnessi*, *H. johnsonorum* and *H. willeyi*, have a white or gray-white ground color with yellow to yellow-orange ridge crests. *Halgerda grafica* has low ridges without tubercles as do *H. gunnessi* and *H. johnsonorum*. Only *H. willeyi* has prominent tubercles. Although both *H. grafica* and *H. johnsonorum* have dark spots or markings in the ridge concavities, only *H. grafica* has the "hieroglyphic markings" described by Basedow and Hedley. These markings consist of a dark spot at the center of the concavity surrounded by dark circles and lines (Fig. 1). The other two species, *H. gunnessi* and *H. willeyi* may also have dark lines or markings, but both lack the associated spots.

The coloration of the mantle edge also distinguishes these four species. *Halgerda grafica* does not have perpendicular dark markings along the mantle edge, but the edge markings of *H. johnsonorum* appear as continuous lines, which extend upward and into the ridge concavities on the dorsum. The dark perpendicular lines on the mantle margin of *H. willeyi* also extend up into the

## DISCUSSION

Although Basedow and Hedley (1905) described the external and radular morphology of *Halgerda grafica*, these authors did not illustrate or describe the reproductive morphology. Despite this, based on the unique color pattern of this species, there is little doubt that the specimens examined for this study are *Halgerda grafica*. Other authors (Coleman 1975, 2001; Kay 1979; Kay and Young 1969; Wells and Bryce 1993) have erroneously attributed the name *Halgerda grafica* to other species. Wells and Bryce, mislabeled a specimen of *Halgerda gunnessi* as *H. grafica*; Basedow and Hedley, 1905; Kay misidentified a specimen of *H. terramtuensis* as *H. grafica*; and Coleman (1975, 2001) misidentified a specimen of *H. willeyi* as *H. grafica*.

Examination of the reproductive morphology reveals similar characters to other *Halgerda* such as a two-part prostate, a long,

ridge cavities, but they are more numerous when compared to *H. graphica*. *Halgerda gunnessi* does not have marginal lines (see Fahey and Gosliner 2001).

The ventral surfaces of the four species are not similar in that there are irregularly scattered dark spots without lines only on *Halgerda graphica*. *Halgerda johnsonorum* and *Halgerda willeyi* have black lines; *H. gunnessi* has no markings on its ventrum.

The coloration on the rhinophores and gills differs among the species. *Halgerda graphica* has dark coloration on the tips of the rhinophores and a dark line on the posterior side. This is similar to *H. gunnessi*. The other species have either dark spots (*H. johnsonorum*, *H. willeyi*) or dark spots plus a dark stripe on the rhinophores (*H. johnsonorum*) and large gills. The gill of *H. graphica* is small and darkly colored. The gill of *H. willeyi* is sparsely pinnate with dark speckles. The gill of *H. johnsonorum* is large and has dark spots, and the gill of *H. gunnessi* is large, feathery and has dark lined branches and a dark tip.

With regard to the internal morphology, *Halgerda graphica* has radular characters similar to those of *H. gunnessi* and *H. willeyi*. All three also have three small outer teeth. *H. johnsonorum* is distinct, having six outer teeth, with the penultimate being bifid. *Halgerda graphica* has two finely denticulate outer lateral teeth; the outer three of *H. willeyi* and *H. gunnessi* are not denticulate.

The reproductive morphology of *Halgerda graphica* is most similar to *H. willeyi*. The obvious differences between the two are that the deferent duct of *H. graphica* is much longer and more convoluted than in *H. willeyi* and the vaginal duct of *H. graphica* is much wider with the vagina, being much larger with tubercular glands on the exterior. A glandular vagina is not found in any of the other three species. Both *Halgerda graphica* and *H. gunnessi* have a vaginal sphincter.

The present study confirms the combination of external and internal morphological characters that identify *Halgerda graphica* and distinguish it from the four externally most similar species. The external characters that distinguish this species in the field are: the "hieroglyphic" yellow and black markings on the dorsum, no dark lines on the mantle edge, dark-tipped rhinophores with a posterior medial line, a small, dark gill and small, dark spots on the ventral surface.

### ***Halgerda dichromis* Fahey and Gosliner, 1999**

(Figs. 4–5)

**MATERIAL EXAMINED.**—V8234, one specimen, dissected, 42 mm, Scottburgh, Kwazulu, Natal, South Africa, 25 m deep, collected by V. Fraser, 15 January 2000; V8233, one specimen, dissected, 20 mm, Park Rynie, KwaZulu, Natal, South Africa, 25 m deep, collected by V. Fraser, 28 December 1999; V8232, one specimen, dissected, 16 mm, Park Rynie, KwaZulu, Natal, South Africa, 25 m deep, collected by V. Fraser, 21 January 2000.

**EXTERNAL MORPHOLOGY.**—The external morphology of the specimens examined for this study are as described by Fahey and Gosliner with some color variation. The variation includes the presence of dark half-lines or spots on the dorsum of some specimens, in place of a heavy, dark line. The more juvenile specimens may not have any dark markings at all. Variations in the external color within this species are shown in Figures 4A–C.

**RADULAR MORPHOLOGY.**—There were no differences noted in the radular morphology between the recent specimens examined (Figs 5A–D) and Fahey and Gosliner's (1999) original description and line drawings. Figure 5A–D are the first SEMs of the radula of this species.

**REPRODUCTIVE SYSTEM.**—There were no differences in the sexually mature specimens examined for this study (Fig. 6) and Fahey and Gosliner's (1999) original description of *Halgerda dichromis*.

**REMARKS.**—*Halgerda dichromis* was described from a single specimen collected in 1980



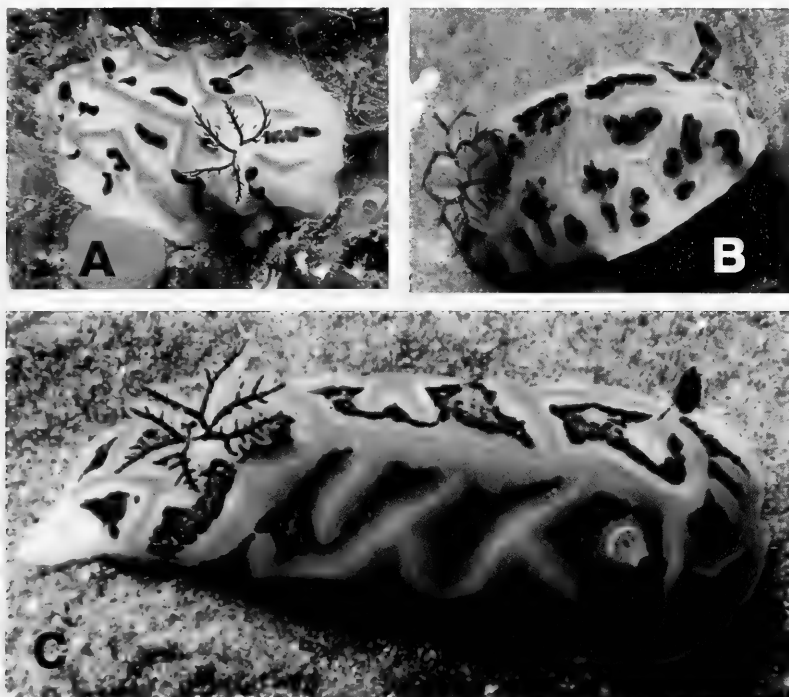


FIGURE 4. Color variation of *Halgerda dichromis*. A–C, Photographed and collected by V. Fraser, 2000.

from Durban Harbor, South Africa. Since the original description, additional specimens have been collected and/or photographed from the same locality (present study) and, thus, allow a further examination of the species.

*Halgerda dichromis* has a variable external coloration (Figs. 4A–C). The coloration of the holotype includes orange and black lines that form a reticulate pattern on the notum (Fahey and Gosliner 1999). Other patterns include having only orange or yellow lines with dark lines or splotches and without dark markings at all, particularly on more juvenile specimens.

*Halgerda dichromis* externally is most similar to *H. formosa* (see Fahey and Gosliner 1999 for details).

#### ***Halgerda okinawa* Carlson and Hoff, 2000**

(Figs. 6–8)

**MATERIAL EXAMINED.**—CASIZ 144092, one specimen, 80 mm, dissected. Izu Peninsula, Japan. 22 m depth, collected by R. Nakano, April 2000; CASIZ 144093, one specimen, 46 mm, dissected. Izu Peninsula, Japan. 20 m depth, collected by R. Nakano, May 2000; CASIZ 144097, one specimen, 50 mm, dissected. Izu Peninsula, Japan. 22 m depth, collected by R. Nakano, April 2000.

**EXTERNAL MORPHOLOGY.**—The external morphology of the specimens examined from the Izu Peninsula have the same range of variation as noted in the original description of *H. okinawa* (Carlson and Hoff, 2000). Those variations include number, length and width of the dark streaks, number of lines on the inner surface of the branchia and presence of a yellow mantle margin on the specimens examined for this study. One of the specimens we examined from the Izu Peninsula has a paler shade of white on the dorsum with pale yellow tubercles (Fig. 7A). The other specimen (Fig.

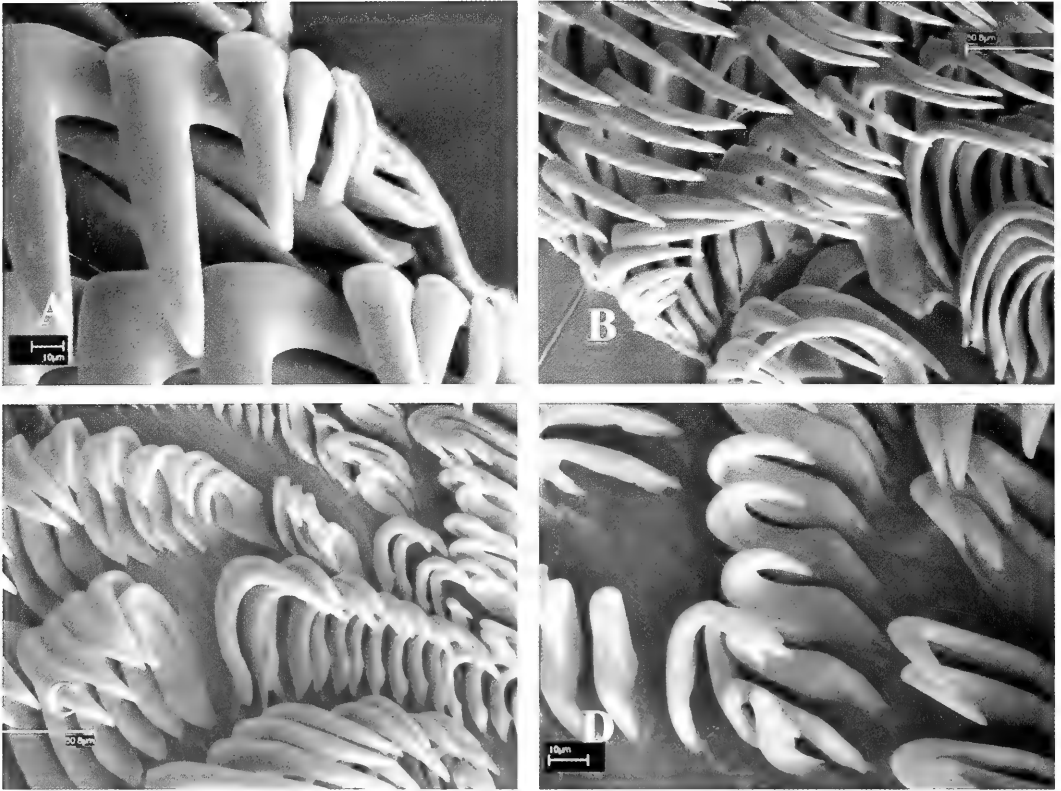


FIGURE 5. Radular morphology of *Halgerda dichromis* (V8233). A. Inner lateral teeth. Scale = 10 µm. B. Middle lateral teeth. Scale = 50.8 µm. C. Middle lateral teeth. Scale = 50.8 µm. D. Outer lateral teeth. Scale = 10 µm.

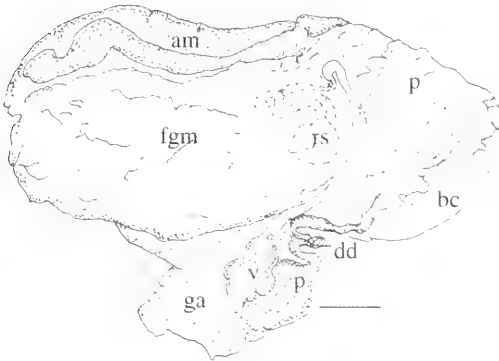


FIGURE 6. Reproductive morphology of *Halgerda dichromis* (V8234). Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.8 mm.

7B) matched the original description from Okinawa. A specimen from Lembeh Strait (Fig. 7C) had few dark lines but more spots than the more commonly found specimen (Figs 7D–E).

**RADULAR MORPHOLOGY.**— There were no differences noted in the radular morphology between the recent specimens examined (Fig. 8) and Carlson and Hoff's (2000) original description.

**REPRODUCTIVE MORPHOLOGY.**— The reproductive morphology of the specimens examined for the present study (Fig. 9) were nearly identical to the original description. The exception is that the vagina is wider in the specimens we examined than was illustrated and drawn by Carlson and Hoff (2000).

**REMARKS.**— Since the original description of *H. okinawa*, additional specimens collected from the Izu Peninsula, Japan and pho-

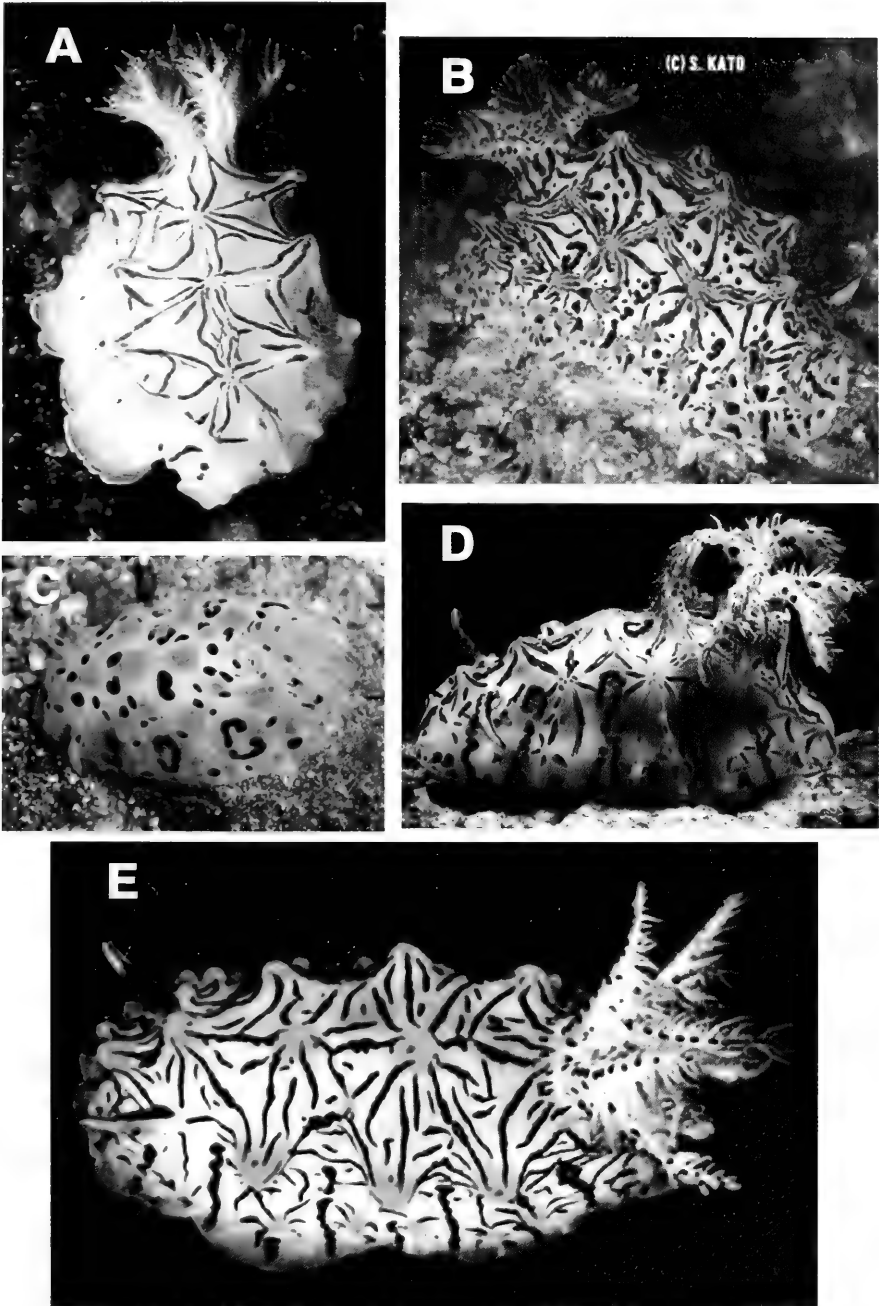


FIGURE 7. Color variation of *Halgerda okinawa*. A. Photographed by Hachijo. B. Photographed by S. Kato, 2001. C. Photographed by Carine Scheurs. D. Photographed by Carlson and Hoff. E. Photographed by R. Bolland.

tographed elsewhere show variation in the external color pattern (Fig. 7C–D). Differences between *Halgerda okinawa* and *H. grafica* were discussed thoroughly by Carlson and Hoff (2000).

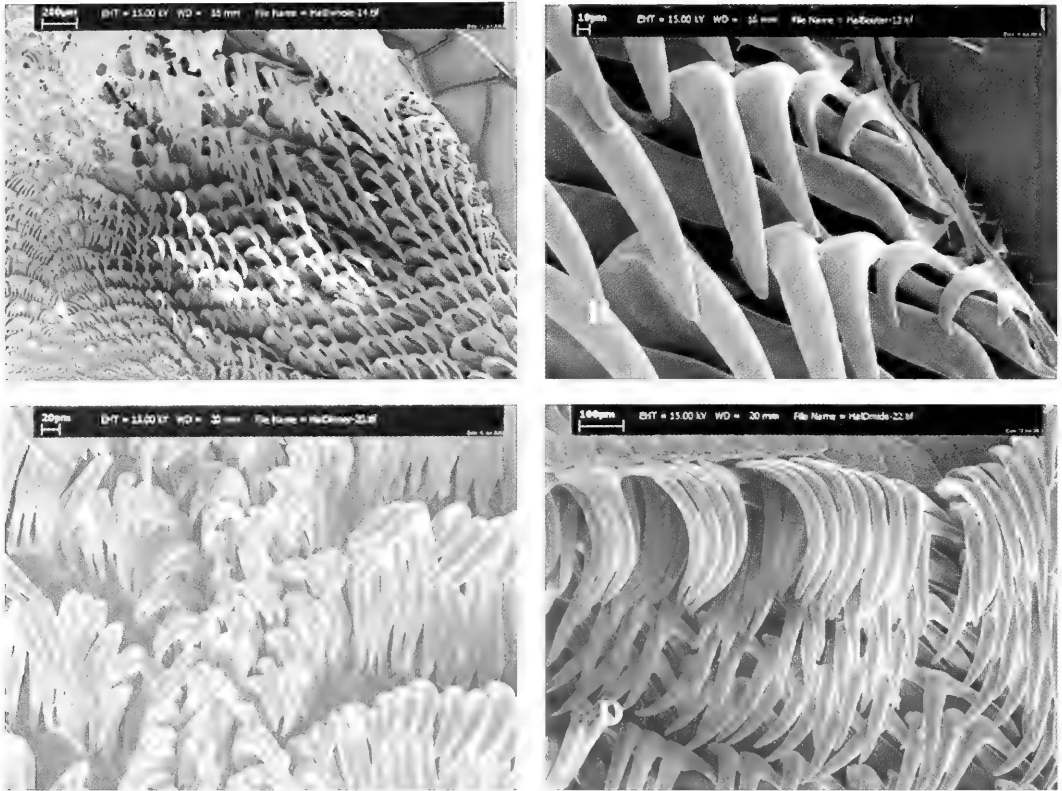


FIGURE 8. Radular morphology of *H. okinawa* (CASIZ 144093). A. Section of the radula. Scale = 200  $\mu$ m. B. Outer lateral teeth. Scale = 10  $\mu$ m. C. Inner lateral teeth. Scale = 20  $\mu$ m. D. Middle lateral teeth. Scale = 30  $\mu$ m.

### *Halgerda willeyi* Eliot, 1904

(Figs 9–11)

= *Halgerda willeyi* in Coleman, 2001, p. 58, center photo, AMPI 117; and in Coleman, 1975 p. 63, Plate 170.

**MATERIAL EXAMINED.**—CASIZ 144095, two specimens: 35 mm, 51 mm (dissected). 20 m depth, collected by R. Nakano, March 2000; CASIZ 144096, three specimens: 25mm, 28 mm, 31 mm (dissected). 21 m depth, collected by R. Nakano, April 2000; CASIZ 144121, one specimen, 40 mm, dissected. 41.5 m depth. 1.3 km ENE Maeki-zaki, Seragaki, Okinawa, Ryukyu Islands, Japan, collected by R. Bolland, January 2001; CASIZ 144123, one specimen, 30 mm. 41.5 m depth. 1.3 km ENE Maeki-zaki, Seragaki, Okinawa, Ryukyu Islands, Japan, collected by R. Bolland, 8 December 2000; CASIZ 134919, one specimen, 74 mm. 43 m depth. 1.3 km ENE Maeki-zaki, Seragaki, Okinawa, Ryukyu Islands, Japan, collected by R. Bolland, 17 August 2000; BMNH, one specimen, 60 mm. Intertidal. Bapper Bay, Aden, Yemen, leg. Sgt. Howse, RAMC, October 1966.

**EXTERNAL MORPHOLOGY.**—Both specimens examined for this study are externally similar to other specimens of *H. willeyi* published elsewhere. However, this species displays great variation in external coloration (Figs. 10A–D; also see Gosliner et al. 1996; Marshall and Willan 1999; Ono 1999; Coleman 1975, 2001; Bolland 2003; Rudman 2003).

**RADULAR MORPHOLOGY.**—There were no differences noted in the radular morphology

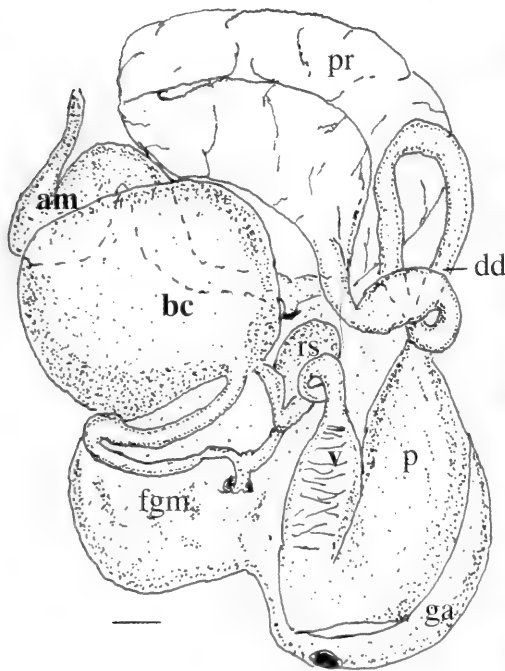


FIGURE 9. Reproductive morphology of *H. okinawa* (CASIZ 144093). Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.5 mm.

between the recent specimens examined (Figs. 11A–D) and in both the original description (Eliot, 1904) and in Rudman's (1978) description.

**REPRODUCTIVE SYSTEM.**— The reproductive morphology of the specimens examined for this study (Fig. 9) match the description provided by Rudman (1978).

**REMARKS.**— *Halgerda willeyi*, at first glance, most closely resembles *H. iota* in external morphology, at least based on the original description of *H. iota* (Yonow 1993). The phylogenetic analysis of *Halgerda* (Fahey and Gosliner 2001) supports a close, morphologically indistinguishable relationship. Regrettably, the reproductive anatomy of *H.*

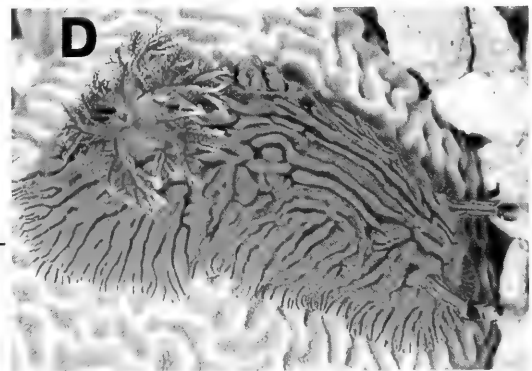
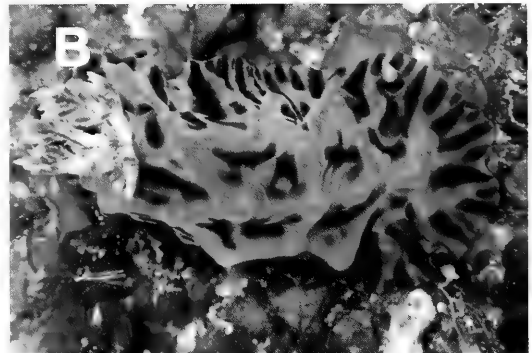
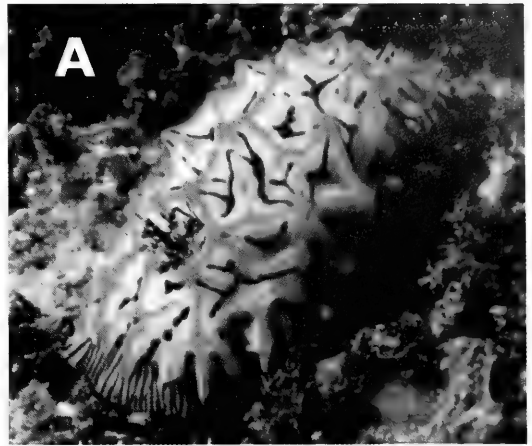


FIGURE 10. Color variation of *Halgerda willeyi*. A. Jervis Bay, NSW, Australia; photographed by L. Wiseman. B. Hachijo Island, Japan; photographed by N. Masatoshi. C. Okinawa; photographed by R. Bolland. D. Lord Howe Island; photographed by Ian Hutton.

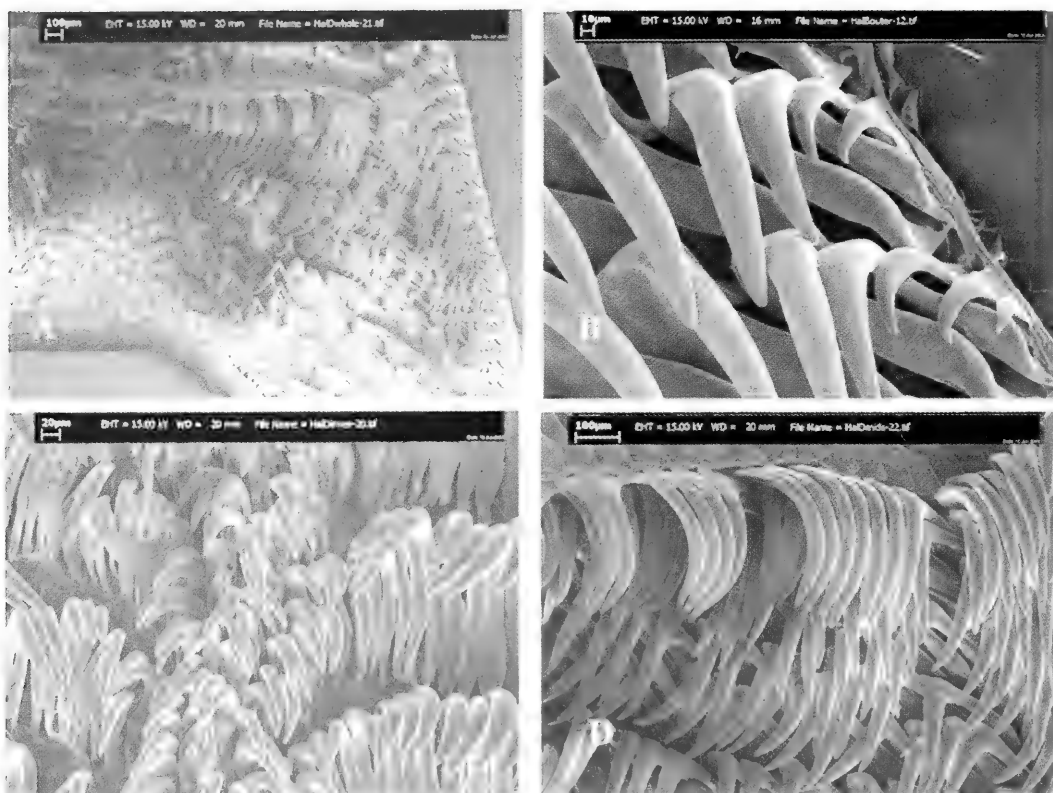


FIGURE 11. Radular morphology of *H. willeyi* (CASIZ 134919). A. Section of the radula. Scale = 200 µm. B. Outer lateral teeth. Scale = 10 µm. C. Inner lateral teeth. Scale = 20 µm. D. Middle lateral teeth. Scale = 30 µm.

*iota* is unknown, and until additional specimens of *H. iota* are collected and the internal anatomy examined, no further comparison of *H. iota* to other species is possible.

*Halgerda willeyi* also is externally similar to other *Halgerda* species. For instance, Carlson and Hoff compared *H. willeyi* to *H. okinawa* and to *H. johnsonorum* (see Carlson and Hoff 2000). There are also some external similarities between *H. willeyi* and *H. elegans* (see Fig. 7C [from Okinawa SlugSite and SeaSlug Forum: photo by B. Picton, SeaSlug Forum, March 8, 2000]); both species have dark lines perpendicular to the mantle edge and yellow-orange lines along the ridge crests. However, the dark marginal lines of *H. elegans* do not extend to as large a degree from the mantle edge throughout the dorsum and into the ridge concavities as they do with *H. willeyi*. The dark lines on specimens of *H. willeyi* are much more numerous, with complex patterns that merge and interweave with the yellow or orange lines all over the dorsum. The yellow ridge crests are the most notable feature of *H. elegans* whereas it is the dark lines with the orange or yellow ridges that are most notable on specimens of *H. willeyi*.

The gill in these two species is quite different as well. In *H. elegans*, it is sparse, irregularly pinnate and has dark coloration encircling the top half of each of the leaves; in *H. willeyi*, is quite bushy, feathered and has a dark line extending the length of each of the leaves.

The rhinophores of the two species also differ in coloration. Those of *H. willeyi* have dark stripes, those of *H. elegans* have black subapical coloration.

The reproductive morphology is vastly different between *Halgerda willeyi* and *H. elegans*. The

most obvious differences are that *H. willeyi* has a large, bulbous penial sheath and a muscularized vagina, whereas *H. elegans* has a tubular penis and a glandular vagina.

Other conspicuous internal differences are noted with the radular morphology of the two species. *Halgerda elegans* has fimbriate outer lateral teeth, with some specimens having multifid teeth with or without pronounced flanges (Bergh 1905; Gosliner and Fahey 1998). The teeth of *H. willeyi* are simple, hamate and the outer two or three are flattened plates (Rudman 1978; Carlson and Hoff 2000).

Although color patterns can vary enormously within *Halgerda* species, as apparent from recently published photographs cited herein, field identifications can be assisted by consideration of not just one or two characters, taken by themselves, but by the combination of characters observed. Examination of the internal morphology will probably be necessary to confirm the more difficult-to-identify specimens.

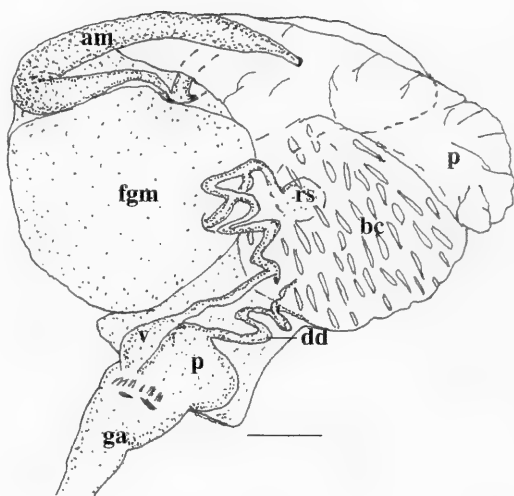


FIGURE 12. Reproductive morphology of *H. willeyi* (CASIZ 144095). Abbreviations: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, ga = genital atrium, p = penis, rs = receptaculum seminis, v = vagina. Scale = 0.8 mm.

#### ACKNOWLEDGEMENTS

The authors are grateful to the following individuals for providing the specimens used for this study: The South Australian Museum; Bob Bolland, Okinawa; Valda Fraser, South Africa and Rie Nakano, Japan. The Queensland Museum, in particular John Hooper, facilitated this work by making the Museum's facilities and resources available. The authors are further indebted to those photographers who generously allowed us to use their photos in this publication (their names are associated with the individual images).

Financial support for this project was provided by the National Science Foundation PEET grant DEB 9978155, "Phylogenetic Systematics of Dorid Nudibranchs" to T.M. Gosliner.

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## The Dangerously Venomous Snakes of Myanmar Illustrated Checklist with Keys

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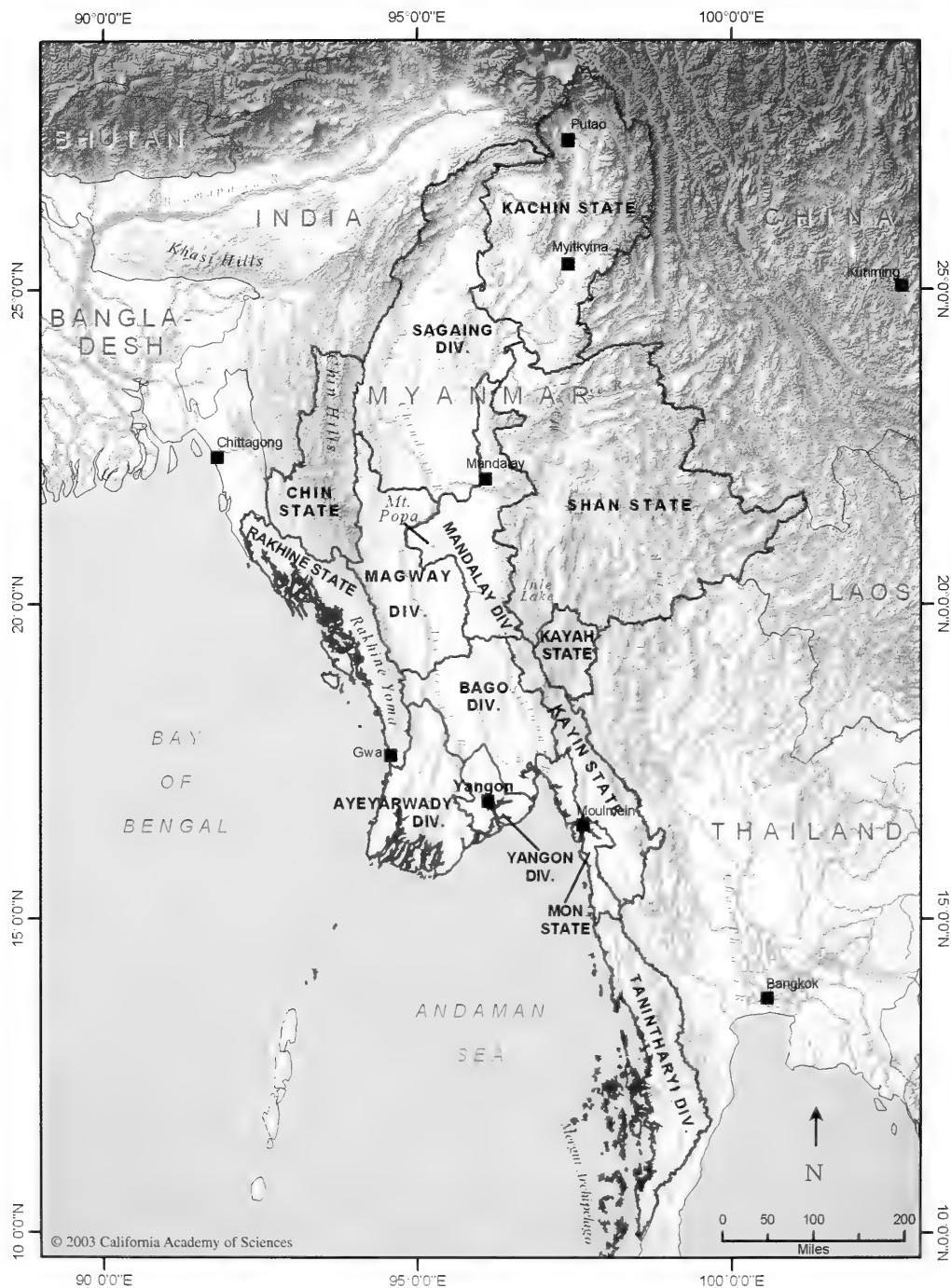
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No fewer than 39 species of dangerously venomous snakes are currently known to inhabit Myanmar and the adjacent coastal waters. Of these, 15 are sea snakes and except for two, *Laticauda colubrina* and *Laticauda laticauda*, none voluntarily come onto land (occasionally, obligate marine species may be carried onto shore during severe weather by wave action or enter river deltas in brackish water). Of the remaining 24 species, all are terrestrial in the sense that none voluntarily enters coastal waters. And, of the terrestrial forms, several, such as *Trimeresurus albolabris*, favor arboreal habitats and are usually found resting on tree limbs. All of the terrestrial species can swim, and some are occasionally found swimming in the rivers and streams as well as in flooded rice paddies.

Two families of dangerously venomous snakes are represented in the Myanmar herpetofauna: Elapidae (cobras, kraits, and coral snakes [subfamily Elapinae], and sea snakes and Australian elapids [subfamily Hydrophiinae]), and Viperidae (true vipers [subfamily Viperinae], pitvipers [subfamily Crotalinae], and *Azemiops* [subfamily Azemiopinae]). Known mildly venomous snakes found there, mostly referred to the very large snake family Colubridae, include the rear-fanged snakes of the Asian vine or whip snake genus *Ahaetulla*, the cat-eyed snakes (genus *Boiga*), the genus *Psammodynastes*, and the aquatic and semi-aquatic snakes of the genera *Enhydria*, *Cerberus*, *Cantoria*, *Fordonia*, and *Bitia*. How dangerous any of these are to humans is still an open matter for research. In a like manner, several of the supposedly nonvenomous colubrids have been shown to have toxic salivas and some should be considered mildly if not dangerously venomous. Among these are members of the genera *Xenochrophis*, *Amphiesma*, and *Rhabdophis*. What we do know is that we often underestimate the severity of many snakebites of both juvenile dangerously venomous and supposedly non-dangerously venomous snakes. Yet, bites of just such animals have been implicated in the deaths of several well-known and knowledgeable professional herpetologists, notably Karl Patterson Schmidt who, in 1957, at the age of 67, was bitten by a juvenile boomslang (*Dispholidus typus*), an African rear-fanged snake, and died one day later, Fred Shannon, M.D., who, in 1965, was bitten by *Crotalus scutellatus*, and died shortly thereafter, Robert Mertens, who was bitten by the African rear-fanged snake, *Thelotornis capensis*, in 1975, and most recently, Joseph Slowinski, who at the age of 38 was bitten by a 30-cm long juvenile krait, *Bungarus* sp.<sup>3</sup>, and died within 48 hours. (See Appendix A for comments relating to procedures for handling venomous snakebites in Myanmar.)

Needless to say, care should always be exercised when handling any snake, even those that are supposedly nonvenomous. And, it must be remembered, it is often difficult to distinguish venomous and nonvenomous species without careful inspection. In Myanmar, for instance, several

<sup>3</sup> Ulrich Kuch (Universität Frankfurt) believes that the specimen, although closely resembling *Bungarus wanghaotingi*, represents a distinct species, which he is in the process of describing (see also remarks under *Bungarus wanghaotingi*).



Topographic and political map of Myanmar

snakes are black with white bandings; among these are *Lycodon zawi*, *Lycodon fasciatus*, *Dinodon septentrionalis*, *Bungarus wanghaotingi*, and *Bungarus flaviceps*. The first three are nonvenomous, the latter two dangerously venomous. Although the five can be told apart fairly readily on the basis of color patterns, once one knows the differences, yet, the only sure way to know whether the snake is a venomous or nonvenomous species is to look at the side of the head just in front of the eye to determine if a loreal scale is present or not. In the illustrated keys that follow, these and other defining characters are clearly noted.

The varied topography and associated ecozones of Myanmar (see Maps p. 408 and 458) support a highly diverse herpetofauna, and we are just now beginning to learn how rich in species it really is. The country has not been carefully studied for many years, and it is a credit to the government of Myanmar and especially to the past and present directors of the Nature and Wildlife Conservation Division, Forest Department, U Uga and U Khin Maung Zaw, that intensive surveys are being conducted throughout the country. Already, significant results have been achieved. Shortly before his death, Joseph Slowinski and his colleague Wolfgang Wüster determined that a hooded cobra found in the Mandalay region represented a distinct species, which they named *Naja mandalayensis*. The importance of this can be quickly appreciated when it is understood that to treat snakebites one most often uses species-specific antivenoms, species-specific in that the antivenom used to treat one kind of snakebite usually will not work for the bites of other species. In Myanmar, for instance, only *Naja kaouthia* antivenom is available for cobra bites. Whether this species-specific antivenom works for other cobra snakebites is unknown. Inasmuch as *N. mandalayensis* was only recently recognized as distinct from *N. kaouthia*, there is no way of telling how many people, bitten by *N. mandalayensis* but treated with *N. kaouthia* antivenom, died but could have been saved had more been known about the species diversity and had the proper antivenom been available. Thus, it is hoped that this contribution will enable those engaged in the study of the fauna in the field and the laboratory to recognize more readily the most dangerous as well as interesting components of that fauna.

In the following checklist, we have made no attempt to provide inclusive synonymies. They are available in the works we do cite, namely, Smith (1926 and 1943), Golay et al., especially the sections by McCarthy and by Toribe (1993), Bauer (1998), McDiarmid, Campbell and Touré (1999) and David and Ineich (1999). Where necessary, we do provide additional references. In the statements on distribution, again we have kept them brief, confining ourselves to country for non-Myanmar localities and, where known, to State or Division within Myanmar.

With respect to species names, we have accepted names for several of the dangerously venomously snakes in Myanmar that have not been widely used in the earlier literature. One notable instance is the many-banded krait, *Bungarus wanghaotingi*, formerly *Bungarus multicinctus*. Recent work indicates that the former is both morphologically and geographically distinct from the latter and is the species occurring in Myanmar (but see footnote 3) and the neighboring region of Yunnan Province, China. *Bungarus multicinctus*, in its restricted sense, is known from eastern China, Taiwan, and to the south and west to Laos. In a like manner, we recognize *Trimeresurus yunnanensis* as distinct from *T. stejnegeri* and, tentatively, have removed the latter from the faunal list for Myanmar. David et al. (2001:219) posit that *T. stejnegeri* (*sensu stricto*) may yet be found in eastern and possibly northern Myanmar (*T. stejnegeri* is known from China [including Yunnan Province], Taiwan, Vietnam, and Laos [see David 2001:218]). If so, we suspect that almost certainly it will be found in northeastern Shan State inasmuch as it has been taken in the vicinity of Menglian, in southwestern Yunnan, not far from the border with Myanmar.

A word about treating snakebites. First, all bites should be taken seriously. It is true that a large percentage of the bites, even by dangerously venomous snakes, are what are known as "dry bites,"

that is bites in which no envenomation takes place. But, it is not always possible to know this in advance. So, best take no chances and seek appropriate medical treatment immediately. Following the section on the identification of dangerously venomous snakes, we have appended a brief statement on how best to proceed in the event of a snakebite. Although more complete instructions are available elsewhere and reference to several published articles is given in the bibliography, we have included as Appendix A a brief statement on the treatment of snakebite in Myanmar prepared in 2000 by Dr. Slowinski for use by members of the Myanmar Herpetological Survey field teams.

This publication was prepared initially for distribution within the Nature and Wildlife Conservation Division of the Forest Department, Ministry of Forestry, Myanmar, and specifically to members of the Myanmar Herpetological Survey field team in Myanmar. First written in April 2002, it has been revised to include new data gathered both by the survey's field team and by the authors' reexamination of both specimens and literature. However, there are a number of people in laboratories in Europe and the United States who are actively engaged in research dealing with the viperid genera *Trimeresurus*, *Ovophis*, and *Protobothrops*, the snakes of the genus *Bungarus*, and the sea snakes, so that the scheme of classification of the venomous snakes as presented here will likely change in the near future.

#### ACKNOWLEDGMENTS

The authors would like to take this opportunity to express their profound appreciation to U Shwe Kyaw, Director General, Forest Department, Ministry of Forestry, and U Khin Maung Zaw, Director of the Division of Nature and Wildlife Conservation, Myanmar, for their ongoing support and encouragement of the Myanmar Herpetological Survey. The survey, initiated by Joseph Bruno Slowinski, Assistant Curator of Herpetology, California Academy of Sciences, in 1998, was initially conceived by U Uga, then Director of the Nature and Wildlife Conservation Division (NWCD). It was with U Uga's encouragement and endorsement that Dr. Slowinski and his colleague, Dr. George R. Zug, Curator of Amphibians and Reptiles at the Smithsonian Institution's National Museum of Natural History, applied for and were granted substantial financial support by the National Science Foundation. The survey was begun in earnest in 1999 at about the same time that U Khin Maung Zaw succeeded U Uga as Director of the NWCD. U Khin Maung Zaw, without hesitation, confirmed his division's confidence in the project. With this support, and with the assignment of several members of the NWCD to the project on a continuing basis, Dr. Slowinski, and other members of the Academy's staff, including Dong Lin, staff photographer, Jens Vindum, Senior Collections Manager in the Department of Herpetology, and two graduate students in Herpetology, Ms. Rhonda Lucas and Ms. Guin Wogan, traveled to Myanmar to conduct field work and, as part of their commitment to the NWCD, to assist in the training of members of its staff in both field and museum techniques.

As noted earlier, in September of 2001, while doing field work in northern Kachin State, Dr. Slowinski was bitten by a krait, *Bungarus* sp., that had just been collected. Because of the field party's isolation, it was not possible to obtain medical help in time and despite valiant efforts to keep him alive, on 12 September 2001, Dr. Slowinski died.

Following the loss of Dr. Slowinski, it was decided by members of the staff of the Academy's Department of Herpetology, again with the encouragement of U Khin Maung Zaw, to continue the project. Thus, we take this opportunity to acknowledge with thanks the contributions that have been and are currently being made to this work by a group of dedicated people both in Myanmar and in the United States: in Myanmar — U Shwe Kyaw, U Khin Maung Zaw, Director of the Division of Nature and Wildlife Conservation; NWCD staff: U Htun Win, Daw Thin Thin, U San Lwin Oo, Sai Wunna Kyi, U Kyi Soe Lwin, U Awan Khwi Shien, and U Hla Tun; in the United States: the late

Joseph Bruno Slowinski, Dong Lin, and Douglas Long. Special thanks must also be accorded U Hla Tun, Dong Lin, Francis Lim, Ashok Captain, Indraneil Das, Nikolai Orlov, and John Tashjian who are responsible for many of the excellent photographs of venomous snakes that are reproduced here. The computer-generated distribution maps were prepared by Michelle S. Koo, the Department of Herpetology's resident Biogeographical Information System Coordinator.

Dr. Indraneil Das, to whom we are indebted for his critical review of the manuscript, also provided us with extensive new information that he has garnered from several sources, including Bauer (1998), McCarthy (1993), Toriba (1993), and his own researches, that either correct or amplify what is known about type localities and the location of holotypes or syntypes of many of the species we deal with here: *Bungarus bungaroides*, *Bungarus fasciatus*, *Laticauda colubrina*, *Laticauda laticaudata*, *Naja kaouthia*, *Ophiophagus hannah*, *Sinomicrurus maclellandi*, *Enhydrina schistosa*, *Hydrophis cantoris*, *Hydrophis fasciatus*, *Hydrophis gracilis*, *Hydrophis obscurus*, *Hydrophis ornatus*, *Hydrophis spiralis*, *Hydrophis stricticollis*, *Kerilia jerdoni*, *Praescutata viperina*, *Daboia russelii*, *Ovophis monticola*, *Protobothrops jerdonii*, *Protobothrops mucrosquamatus*, *Trimeresurus erythrurus*, *Trimeresurus popeiorum*, and *Trimeresurus stejnegeri*. Dr. Das offered that we could include his data here, but we have chosen not to do so because shortly he will be issuing an updated checklist of Indian reptiles and will include these data in that work. We do want to express our deepest appreciation for his generosity and now look forward, eagerly, to his publication.

At this time we also want to acknowledge ERSI's Conservation Technology Support Program (CTSP) for generously providing both the software and training that have enabled us to prepare the distribution maps that accompany this report.

Lastly, we want to express our appreciation to Dr. Michele L. Aldrich who, with her usual editorial acumen, read the manuscript and caught more errors than we wish to acknowledge.

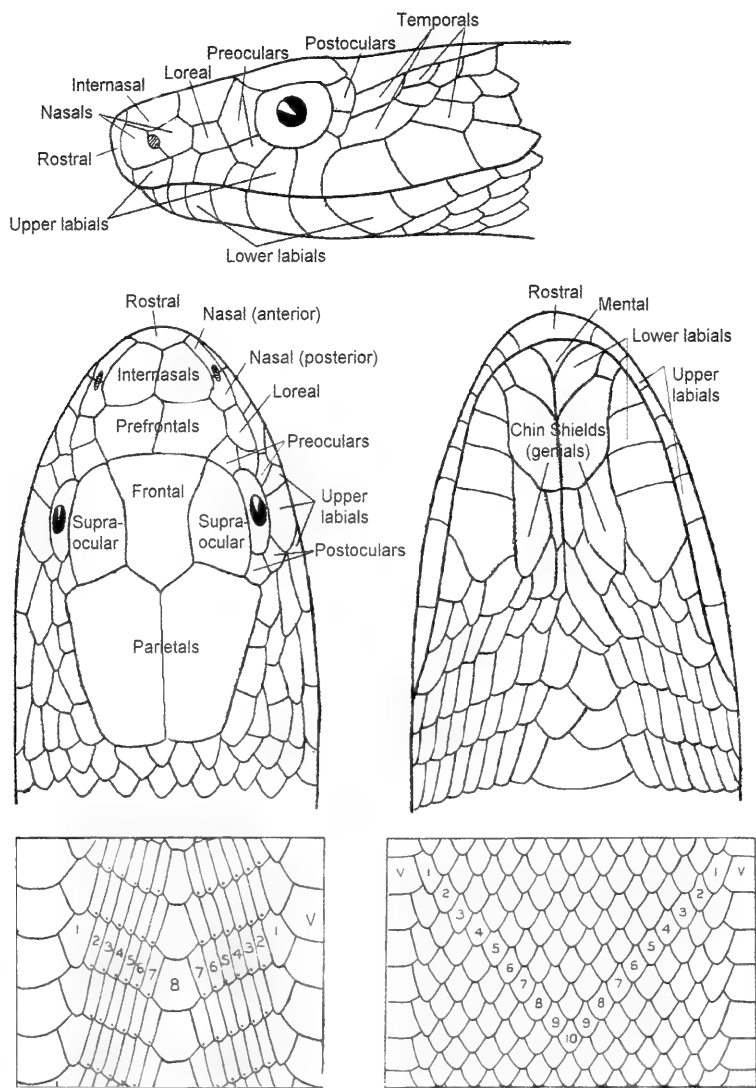
The Myanmar work has been supported by a grant from the National Science Foundation, DEB 9971861. Additional funding has been provided by the California Academy of Sciences' Research Division Inhouse Research and Geraldine K. Lindsay Funds and the Department of Herpetology's Dufflebag Fund.



This contribution is dedicated to the  
memory of

**Dr. Joseph Bruno Slowinski**

who lost his life in the pursuit of an  
understanding of the Myanmar  
herpetofauna, with special reference to  
its dangerously venomous snakes.



Diagrams of head and body scutellation in a typical snake.  
Head shields: (A) Lateral view; (B) Dorsal view; (C) Ventral view  
Body scales (numbers indicate best method for counting body scales):  
Scales arranged in (A) oblique rows; (B) parallel rows.  
(Modified from Smith [1943])

CHECKLIST AND KEYS TO THE DANGEROUSLY VENOMOUS SNAKES OF MYANMAR

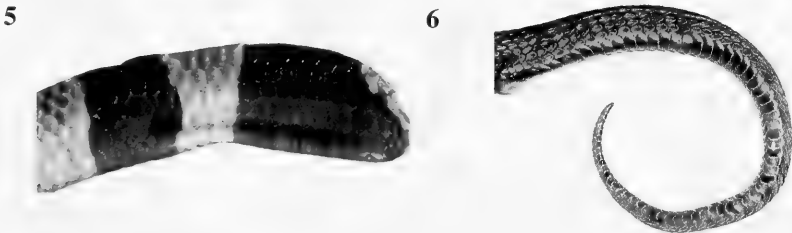
Key to the Genera and Species of Venomous Snakes of Myanmar<sup>1</sup>

- 1a. Pupil of eye round; loreal scale absent (Fig. 1); poison fangs short, permanently erect; maxillary bone elongate, usually with several small teeth behind the front fangs (Family Elapidae, including cobras, coral snakes, and sea snakes) ..... 2
- 1b. Pupil of eye vertically elliptical; loreal scale present (Fig. 2) or, if absent, then upper surface of head either covered by small scales (Fig. 3) or, if covered by large, symmetrical shields, then a deep sensory pit present immediately behind the nostril (Fig. 4) (also present in many in which the head is covered by small scales); poison fangs variable in length, fixed to a short moveable maxillary bone that allows for rotation of the fangs backward when the mouth is closed; no post-fang teeth behind fangs (Family Viperidae)..... 29



Left to right: (1) Loreal absent, nasal in contact with preocular (*Bungarus wanghaotingi*); (2) loreal present, separating nasal and preocular (*Azemiops feae*); (3) head covered with small scales, sensory pit absent (*Daboia russelii*); (4) head covered with small scales, sensory pit present (*Trimeresurus erythrurus*)

- 2a. Tail flattened laterally, oar-like (Fig. 5) ..... 13
- 2b. Tail rounded, tapering (Fig. 6) ..... 3

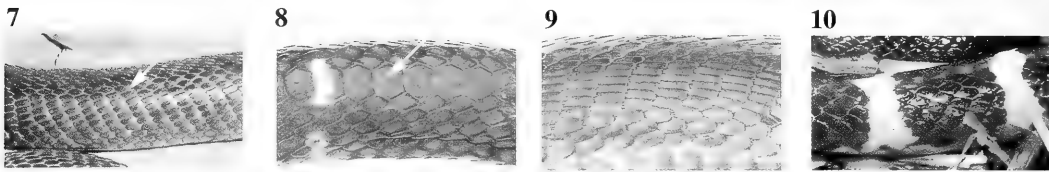


(5) Oar-like tail (*Laticauda laticaudata*), which is characteristic of all venomous sea snakes versus (6) a tapering or at least non-flattened tail (*Trimeresurus purpureomaculatus*), characteristic of all terrestrial snakes

- 3a. Vertebral series of scales not enlarged (Fig. 7); scales on sides of body obliquely arranged or not. .... 4
- 3b. Vertebral series of scales enlarged (Fig. 8), distinctly larger than scales on sides of body; scales on sides of body not obliquely arranged ..... 9

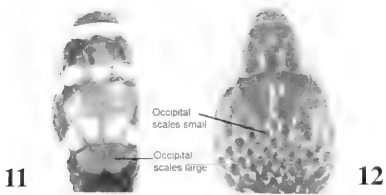
<sup>1</sup> In preparing this key and the checklist that follows, we have been guided by the latest revisionary studies, but we have also taken a conservative position because of the nature of the animals with which we are working. Thus, although we accept McDowell’s argument that among the sea snakes *Enhydrina schistosa* should be referred to the genus *Disteira* and *Thalassophis viperina* to *Lapemis*, we have not done so here. Most of the medical and general literature dealing with sea snakes still refer to *Enhydrina schistosa* and *Thalassophina viperina*. Also, we have, rather arbitrarily, chosen to accord all recognizably distinct allopatric subspecies full species status rather than get embroiled in endless arguments of why raise one subspecies to full species status but retain another as a subspecies, though both can be readily, though differentially, diagnosed taxonomically. Arguments as to what constitutes a biological “species” versus “subspecies” are pointless and are usually based on an arbitrary assessment by a given worker on just how “important” a given character or character state is in inferring the “closeness” of biological affinities, i.e. the genealogical relationships among the parties.

- 4a. Scales on sides of body obliquely arranged (Fig. 9), pointing backward and downward, most distinct on sides of neck; scales in 15 to 23 longitudinal rows around midbody ..... 5
- 4b. Scales on sides of body not obliquely arranged (Fig. 10), in straight longitudinal rows; scales in 13 to 15 longitudinal rows around midbody ..... 7



Left to right: (1) Vertebral row of scales not enlarged, (2) vertebral scales distinctly enlarged (*Bungarus wanghaotingi*); (3) body scales, except for outer two or three horizontal rows, obliquely arranged (*Naja mandalayensis*); (4) body scales in parallel rows, not obliquely arranged

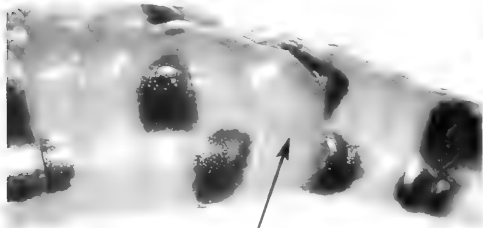
- 5a. Scales in 15 longitudinal rows at midbody; a pair of large occipital shields present (Fig. 11). ..... *Ophiophagus hannah*
- 5b. Scales in 19–25 longitudinal rows at midbody; no enlarged occipital shields (Fig. 12). .... 6



Head scutellation in cobras: (11) Paired occipital shields present (*Ophiophagus hannah*); (12) No enlarged occipital shields (*Naja* sp.)

- 6a. Usually distinct dark markings on the hood; throat cream colored, often with a pair of well-defined lateral spots; when present, only a single dark band on the throat, otherwise venter either pale or gradually increasingly cloudy with dark pigment towards the rear, posteriorly venter often totally dark ..... *Naja kaouthia*
- 6b. No or only faintly distinct markings on the hood; throat extensively darkly mottled anterior to first dark throat band, mottling obscuring the throat spots characteristic of most species of *Naja*; at least two distinct dark bands on venter, one on the throat followed by a second on anterior third of venter; venter otherwise pale with some dark mottling *Naja mandalayensis*

- 7a. Anal scute divided (Fig. 13). .... 8
- 7b. Anal scute single (Fig. 14); preocular scale present; snout and venter free of dark pigment (no confirmed records for Myanmar). .... *Calliophis bivirgatus*



13

divided anal scute



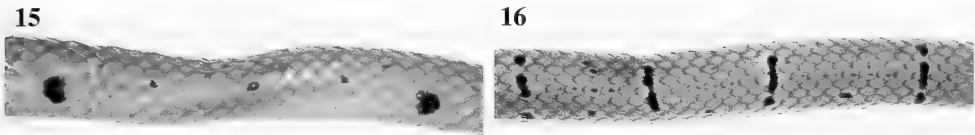
14

undivided anal scute

(13) Anal plate divided (*Sinomicrurus maclellandi*); (14) Anal plate undivided (single) (*Calliophis bivirgata*)

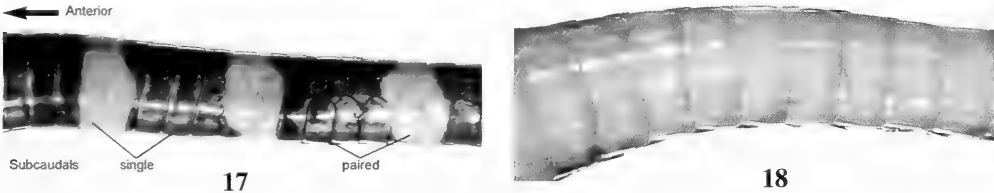


- 8a. Pattern on dorsum characterized by small black spots (Fig. 15), sometimes forming longitudinal stripes, with two black bands or rings on tail, one at base and one at the tip; one to three small maxillary teeth behind fangs ..... *Calliophis maculiceps*
- 8b. Pattern on dorsum characterized by small but distinct black vertical bars on sides (Fig. 16), sometimes forming crossbars, with two black rings on tail; no maxillary teeth behind fangs ..... *Sinomicrurus macclellandi*



Dorsal color patterns: (15) Spotted pattern of *Calliophis maculiceps*;  
(16) Barred pattern of *Sinomicrurus macclellandi*

- 9a. Scales in 13 longitudinal rows at midbody; terminal caudal scales paired ..... *Bungarus flaviceps*
- 9b. Scales in 15 longitudinal rows at midbody; terminal caudal scales single or paired ..... 10
- 10a. Subcaudal scales usually paired, occasionally some unpaired anteriorly (Fig. 17), but terminal scales always paired. .... *Bungarus bungaroides*
- 10b. Subcaudal scales entire (Fig. 18), not paired ..... 11

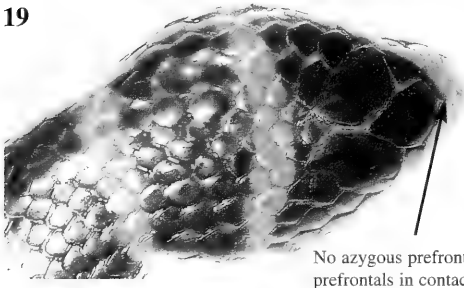


Subcaudal scutes: (17) Mixed paired and unpaired (*Bungarus bungaroides*);  
(18) All single (unpaired) (*Bungarus fasciatus*)

- 11a. Tail tapers to a point (Fig. 6); neural processes of vertebrae not enlarged vertically and do not produce a distinct ridge down the back; dorsal crossbars do not encircle body; belly white
- 11b. Tail ends bluntly, not pointed; neural processes of vertebrae enlarged vertically and produce a distinct ridge down the back; body marked with alternating black and yellow bands that completely encircle body ..... *Bungarus fasciatus*
- 12a. 27–48 narrow white crossbars on back, crossbars narrowest middorsally, expanding on sides ..... *Bungarus wanghaotingi*
- 12b. 11–14 broad white, black-spotted crossbars on back, crossbars as broad as or broader than the darker interspaces ..... *Bungarus magnimaculatus*
- 13a. Ventral scales large, one-third to one-half the width of the body; maxillary bone extends forwards beyond palatines; nostrils lateral, nasal scales separated by internasals. .... 14
- 13b. Ventral scales small, less than one-fourth width of body, often smaller than or at least not larger than adjacent body scales; maxillary bone usually does not extend forwards beyond palatine (exceptions, *Kerilia jerdoni*, *Hydrophis gracilis* and *H. cantoris*); nostrils variable, internasal scales absent, nasal scales in contact with one another. .... 15

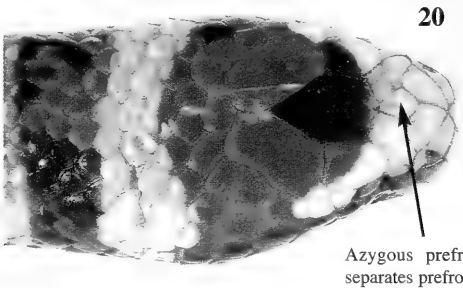
- 14a. Scales in 19 longitudinal rows at midbody; no azygous (median) prefrontal scale (Fig. 19)  
..... *Laticauda laticaudata*  
14b. Scales in 21–25 longitudinal rows at midbody; an azygous (median) prefrontal scale usually  
present (Fig. 20) ..... *Laticauda colubrina*

19



No azygous prefrontal;  
prefrontals in contact

20

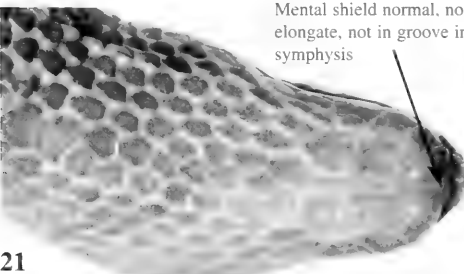


Azygous prefrontal  
separates prefrontals

Azygous prefrontal shield: (19) Absent in *Laticauda laticaudata*;  
(20) Present in *Laticauda colubrina*

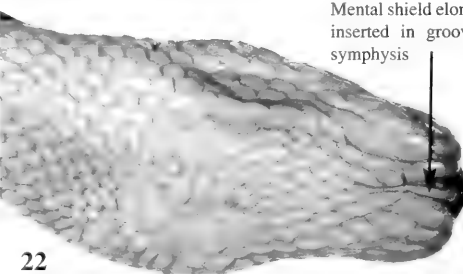
- 15a. Ventral scales small but distinct, undivided by a median groove or, if divided posteriorly, the  
two halves either apposed or alternating with one another, then head very small and body long  
and very slender anteriorly. .... 16  
15b. Ventral scales, if distinct, then either divided by a median groove or smaller than adjacent  
body scales. .... 28  
16a. Scale rows in 23 or fewer rows around midbody; maxillary bone extends forwards beyond  
palatine; little or no space (diastema) separates fangs from smaller maxillary teeth .....  
..... *Kerilia jerdoni*  
16b. Scale rows in 25 or more rows around midbody (but often fewer around neck); maxillary bone  
does not extend forwards beyond palatine (except in *H. gracilis* and *H. cantoris*); a distinct  
space (diastema) separates fangs from smaller maxillary teeth ..... 17

- 17a. Mental scale normal (Fig. 21) ..... 18  
17b. Mental scale elongate, partially hidden in groove in the symphysis (Fig. 22); ventrals uniform  
in size; 3–5 small maxillary teeth behind fangs ..... *Enhydrina schistosa*



21

Mental shield normal, not  
elongate, not in groove in  
symphysis

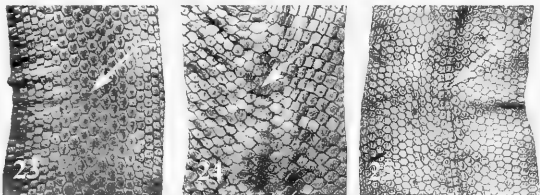


22

Mental shield elongate,  
inserted in groove in  
symphysis

Mental shield: (21) Mental normal, neither elongate nor partially hidden in groove in the symphysis (*Hydrophis*);  
(22) Mental elongate, hidden in groove of symphysis when mouth is closed (*Enhydrina schistosa*)

- 18a. Ventral scales broad anteriorly, reduced posteriorly and not distinct from adjacent scales (Fig. 23); 5 maxillary teeth behind fangs ..... *Thalassophina viperina*
- 18b. Ventral scales slightly distinct from adjacent scales and of uniform shape throughout irrespective of their size, (Fig. 24); 1–18 maxillary teeth behind fangs ..... 19



Ventral scales: (23) Undivided and indistinguishable from adjacent scales (*Lapemis hardwickii*); (24) Usually distinguishable from adjacent scales (*Hydrophis cyanocinctus*); (25) Divided by a longitudinal groove (*Hydrophis gracilis*)  
(From Smith, 1926, pl. 1, figs. 3, 4, and 1.)

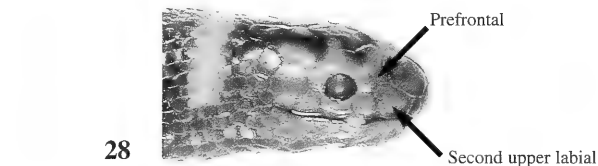
- 19a. Head very small, body elongate, anterior fifth slender, about same diameter as head (Fig. 27); ventrals small, posterior series usually divided by a longitudinal groove (Fig. 25), the two halves either apposed or alternating with one another; maxillary bone extends as far forward as anterior tip of palatine or beyond; 5–6 small maxillary teeth behind anterior fangs . . . 20
- 19b. Head not distinctly reduced, body not particularly slender anteriorly (Fig. 26); ventrals small, usually distinct throughout and entire, only rarely are a few divided by a longitudinal groove; maxillary bone does not extend forward beyond palatine; 1–18 small maxillary teeth behind anterior fangs ..... 23



Head and body dimensions: (26) head and anterior portion of body not distinctly narrowed (*Hydrophis spiralis*); (27) head and anterior fourth of body slender (*Hydrophis atriceps*)

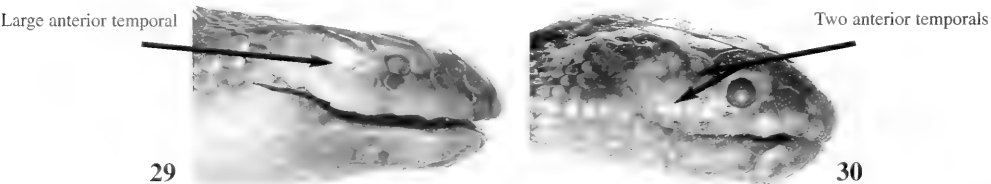
- 20a. Ventral scales entire throughout; head black. .... 21
- 20b. Ventral scales anteriorly entire, posteriorly at least some divided by a longitudinal groove (Fig. 25); head color variable. .... 22
- 21a. Scales in 28–33 rows on neck, 49–58 around midbody; ventrals 414–514  
..... *Hydrophis (Hydrophis) fasciatus*
- 21b. Scales in 25–30 rows on neck, 39–49 around midbody; ventrals 323–452  
..... *Hydrophis (Hydrophis) atriceps*

- 22a. Prefrontal scale usually in contact with second upper labial (Fig. 28); ventrals 220–350; 17–23 scale rows around neck . . . . . *Hydrophis (Hydrophis) gracilis*
- 22b. Prefrontal scale usually in contact with third upper labial; ventrals 404–468; 23–25 scale rows around neck, rarely 21 . . . . . *Hydrophis (Hydrophis) cantoris*



(28) Lateral view of head of *Hydrophis gracilis* showing contact of prefrontal with second upper labial; third and fourth upper labials border eye

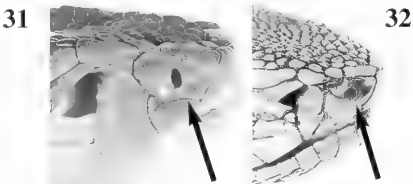
- 23a. Scales at midbody rounded or bluntly pointed posteriorly, feebly to distinctly imbricate; 1–8 maxillary teeth behind anterior fangs . . . . . 24
- 23b. Scales at midbody feebly imbricate or juxtaposed, quadrangular to hexagonal in shape; 8–18 maxillary teeth behind anterior fangs . . . . . 26
- 24a. No enlarged anterior temporal scute, temporals small, scarcely distinguishable from surrounding scales; 1–2 maxillary teeth behind anterior fangs . . . . . *Disteira nigrocincta*
- 24b. Normally one large anterior temporal scute (Fig. 29), clearly distinguishable from ordinarily scales, occasionally extending downward to border of lip . . . . . 25
- 25a. 19–23 scale rows on neck; ventrals 300–338 . . . . . *Hydrophis (Hydrophis) obscurus*
- 25b. 25–31 scale rows on neck; ventrals 295–362 . . . . . *Hydrophis (Leioselasma) spiralis*
- 26a. Normally two or three anterior temporals (Fig. 30); ventrals less than 350; head olive or gray in adult; 40–60 dark crossbands or rhomboidal spots, wider than light interspaces, becoming obscure with age; below yellowish or whitish . . . . . 27
- 26b. Normally one anterior temporal (Fig. 29); ventrals 374–452; head dark gray or olive, or, if blackish dorsally, with yellow mottling on snout and sides; dorsum with 45–65 dark bands, becoming obscure with age; below pale; dentary teeth 19–22 . . . . . *Hydrophis (Aturia) stricticollis*



(29) Single large anterior temporal (*Hydrophis spiralis*); (30) Two anterior temporals (*Hydrophis caeruleus*)

- 27a. Pale gray or olive above to almost white, with broad dark bars or rhomboidal spots separated by narrow interspaces; yellowish or whitish below; head olive; 8–13 maxillary teeth behind fangs . . . . . *Hydrophis (Aturia) ornatus*
- 27b. Bluish-gray above, yellowish or whitish below, with 40–60 broad bands about twice as broad as interspaces; markings indistinct on older individuals, which are almost uniform gray; head

- dark gray to black, occasionally with light curved marking in young; 13–18 maxillary teeth behind fangs. . . . . *Hydrophis (Aturia) caerulescens*
- 28a. Olive to gray above, whitish below, 35–55 narrow dark bands, occasionally uniform dark gray; midventral rows of body scales larger than adjacent lateral and dorsolateral scales; ventral scutes, if discernable, not divided by a longitudinal groove; 3–6 small maxillary teeth behind fangs; no discernable series of midventral scutes . . . . . *Lapemis hardwickii*
- 28b. Bicolored, ordinarily black above, yellow below, with some variation in which yellow extends further up on the sides and the black is restricted to a wide middorsal stripe; sometimes black bars on belly; tail mottled yellow and black; ventral scutes, when distinct, divided by a longitudinal groove; 8–10 maxillary teeth . . . . . *Pelamis platurus*
- 29a. Loreal pit present (Fig. 4); head distinctly triangular in shape. . . . . 31
- 29b. Loreal pit absent (Figs. 2–3); head distinct from neck but variable in shape . . . . . 30
- 30a. Loreal scale present but small (Fig. 2); head scutes large, symmetrical; dorsal scales in 17 longitudinal rows at midbody . . . . . *Azemiops feae*
- 30b. Loreal scale absent (Fig. 3); both top and sides of head covered by small, imbricate, distinctly keeled scales, except for the small, strongly crescentric supernasal, the large undivided nasal, and 10–12 upper labials . . . . . *Daboia russelii*
- 31a. First upper labial completely separated from nasal by a distinct suture (Fig. 31) . . . . . 32
- 31b. First upper labial partially or completely fused to nasal (Fig. 32) . . . . . 39



Nasal and first upper labial scales in *Trimeresurus* and *Ovophis*: (31) Nasal completely separated from first upper labial by suture (*Ovophis monticola*); (32) Nasal partially or completely fused to first upper labial (*Trimeresurus purpureomaculatus*)

- 32a. Body scales in 17–21 (rarely 23) longitudinal rows at midbody . . . . . 35
- 32b. Body scales in 23–27 (rarely 21) longitudinal rows at midbody . . . . . 33
- 33a. Ventrals more than 190 . . . . . 34
- 33b. Ventrals fewer than 190 (137–176 for Myanmar and adjacent areas of India, Thailand, and China, 127–144 further east); subocular scales usually fragmented into smaller scales . . . . . *Ovophis monticola*
- 34a. 8–10 scales in a line between supraoculars; ventrals 201–212; subcaudals 66–78; outermost one or two rows of body scales (those bordering ventrals) smooth, all other rows strongly keeled . . . . . *Protobothrops kaulbacki*
- 34b. 14–16 scales in a line between supraoculars; ventrals 200–218; subcaudals 76–91; outermost rows of body scales (those bordering ventrals) keeled . . . . . *Protobothrops mucrosquamatus*
- 35a. Body scales in 17 longitudinal rows at midbody; ventrals fewer than 150; bicolored ventrolateral stripe present in both males and females. . . . . *Trimeresurus medoensis*
- 35b. Body scales in 19–21 longitudinal rows at midbody; ventrals more than 150; ventrolateral stripe variable . . . . . 36

- 36a. Dominant background body color green; dorsum of head green ..... 37
- 36b. Dominant background body color variable, greenish or olive above with series of transverse, rhomboidal, or irregular reddish brown to black spots or blotches, to entirely black; dorsum of head black with symmetrically arranged yellow markings; belly yellow with black spotting ..... *Protobothrops jerdonii*
- 37a. Scales in 19 (rarely 21) longitudinal rows at midbody and 19 (–21) on neck; ventrals 155–165 (–170); subcaudals (58–) 61–68 (in Myanmar from Kachin and ?Chin States); ventrolateral stripe bicolored (orange or brown below, white above) in males, white or absent in females ..... *Trimeresurus yunnanensis*
- 37b. Scales in 21 longitudinal rows at midbody (21–23 on neck); ventrolateral stripe bicolored (orange or brown below, white above) in males, bicolored or white only in females ..... 38
- 38a. Ventrals: males 161–172, females 157–169; subcaudals: males 71–79, females 58–74; hemipenes long, slender, extending to level of 20<sup>th</sup>–25<sup>th</sup> subcaudal scale, forked at level of fifth subcaudal scale, without spines (in Myanmar, known from vicinity of Mergui); ventrolateral stripe bicolored (orange or brown below, white above) in males, white in females ..... *Trimeresurus popeiorum*
- 38b. Ventrals (for Chinese specimens only [after Zhao et al. 1998 and David et al. 2001]): 154–172; subcaudals: 43–75; hemipenes short, stout, extending to 10<sup>th</sup> subcaudal plate, forked at level of fifth subcaudal scute, spinose (species not presently known from Myanmar but possibly in north and east); ventrolateral stripe bicolored (orange or brown below, white above) in males, bicolored or white in females. .... *Trimeresurus stejnegeri*
- 39a. Scales in 21 (rarely 19) longitudinal rows at midbody; temporal scales smooth or weakly keeled; dorsum of head uniform green; tail usually not spotted with brown (in juveniles, tip of tail brown) ..... *Trimeresurus albolabris*
- 39b. Scales 23 or more longitudinal rows at midbody; temporal scales keeled; tail usually spotted with brown ..... 40
- 40a. Head uniform green; body green above, pale green to yellowish below; ventrals: males, 153–174, females, 151–180; subcaudals: males, 62–79, females, 49–61 ..... *Trimeresurus erythrurus*
- 40b. Head and body brown to purplish-brown above, whitish to brown below; ventrals: males, 160–179, females 168–183; subcaudals: males 74–76, females 56–63 ..... *Trimeresurus purpureomaculatus*

## CHECKLIST OF THE DANGEROUSLY VENOMOUS SNAKES OF MYANMAR

### FAMILY ELAPIDAE

#### Subfamily ELAPINAE

#### Genus *Bungarus* Daudin, 1803

*Bungarus* Daudin, 1803. (Type species: *Bungarus annularis* Daudin, 1803 [= *Pseudoboa fasciata* Schneider, 1801]).

#### *Bungarus bungaroides* (Cantor, 1839)

*Elaps bungaroides* Cantor, 1839:33. (Type locality: Cherra Punghi, Khasi Hills, Meghalaya State, India; Holotype: BMNH 1946.1.17.91).

*Bungarus bungaroides*, Smith, 1943:410.— Toriba, 1993:118.— David and Ineich, 1999:66.

**DIAGNOSTIC CHARACTERS.**— Dorsal scales in 15 longitudinal rows at midbody; subcaudal scutes ordinarily divided anteriorly, but occasionally some scutes may be single, but always divided near the tip; ventrals 220–237; subcaudals 44–51; dorsum black with a series of very narrow white to pale yellowish lines or crossbars; on the belly, the light crossbars widen to form distinct transverse bars. Total length<sup>1</sup> 1400 mm; tail length 160 mm (largest male).

**DISTRIBUTION.**— MYANMAR (Map p. 458): Kachin State. ELSEWHERE: India (Sikkim; Assam [Khasi Hills]); Cachar.

**HABITAT.**— Historically recorded in northern Myanmar (Smith 1940), this species has been documented at elevations of 2040 m (Boulenger 1896:371). In Myanmar, to date, this species has been found only in the subtropical forests of extreme northern Myanmar.

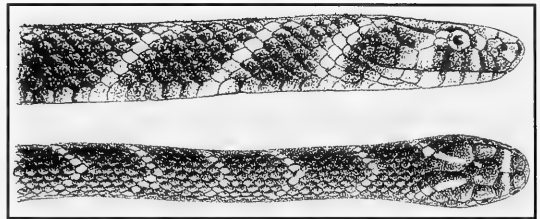
#### *Bungarus fasciatus* (Schneider, 1801)

*Pseudoboa fasciatus* Schneider, 1801:283 (Type locality: Mansoor, Cottah, Bengal, India; Holotype: based on Russell, 1796:3 and pl. iii).

*Bungarus fasciatus*, Smith, 1943:411.— Toriba, 1993:119.— David and Ineich, 1999:68.

**DIAGNOSTIC CHARACTERS.**— Dorsal scales in 15 longitudinal rows at midbody; subcaudal scutes undivided throughout; middorsal row of scales (vertebrals) strongly enlarged, as broad as or broader than long; tail end blunt; distinct vertebral ridge down the back formed by the neural processes of the vertebrae; ventrals 200–234; subcaudals 23–39; pattern of black and yellow bands, all of which encircle body. Total length recorded to 2125 mm, said to be rare over 1800 mm. (Smith, 1943:412.)

**DISTRIBUTION.**— MYANMAR: widely distributed (Ayeyarwady Division, Kachin State,



*Bungarus bungaroides* (from Boulenger 1893, pl. 18, fig. 5).



*Bungarus fasciatus*. Photo by Francis Lim.

<sup>1</sup> Body and tail lengths are mostly taken from Smith (1943).



Magway Division, Mandalay Division, Rakhine State, Yangon Division). ELSEWHERE: central and northeastern India throughout all of southeastern Asia including southern China, Thailand, Cambodia, Laos, Vietnam, and Malaysia, to western Indonesia (Java, Sumatra, Kalimantan).

**HABITAT.**— In Myanmar, this species has been found primarily in low-lying regions with elevations from close to sea level to around 300 m. Historical records, however, indicate elevations up to 2300 m (Schleich and Kästle 2002). Most of the individuals encountered have been found in degraded habitat in the vicinity of villages and agriculture (including paddy). Several have been found along or near streams. Elsewhere, it is recorded from a diverse array of habitat types (see Pawar and Birand 2001; Das 2002; Schleich and Kästle 2002). Active at night.

### *Bungarus flaviceps* Reinhardt, 1843

*Bungarus flaviceps* Reinhardt, 1843:267, pl. iii, fig. 4 (Type locality: Java; Holotype: ZMC R65301).— Smith, 1943:410.— Toriba, 1993:119.— David and Ineich, 1999:68.

**DIAGNOSTIC CHARACTERS.**— Dorsal scales in 13 longitudinal rows at midbody; expanded neural crest of vertebrae forms distinct ridge down back and tail; subcaudal scutes undivided, anteriorly those near the tip divided; ventrals: ♂ 220–236, ♀ 193–217; subcaudals: ♂ 47–53, ♀ 42–54. Black above; orange-yellow dorsal stripe often present; interstitial skin orange-yellow giving appearance of longitudinal stripes; head orange-yellow; tail and posterior part of body orange-yellow; belly orange or yellow, sometimes edged with brown. (After Smith, 1943:411.) Total length 1850 mm; tail length 220 mm.



*Bungarus flaviceps*. Photo by Francis Lim.

**DISTRIBUTION.**— MYANMAR (Map p. 458): Tanintharyi Division. ELSEWHERE: Thailand, Malaysia, Cambodia, Vietnam, western Indonesia.

**HABITAT.**— In Borneo and Thailand this species is found primarily in forested areas from sea level to around 900 m in elevation. In Sumatra, it is reported to inhabit low lying hills with a preference for tropical wet forests (David and Vogel 1996). It is generally found under leaf litter and beneath logs. Active at night (Cox et al 1998; Stuebing and Inger 1999).

**REMARKS.**— In Myanmar, this widely distributed Malaysian species has been recorded only from the extreme south, in the vicinity of Myeik (formerly Mergui) and Pyin Mountain.

### *Bungarus magnimaculatus* Wall and Evans, 1901

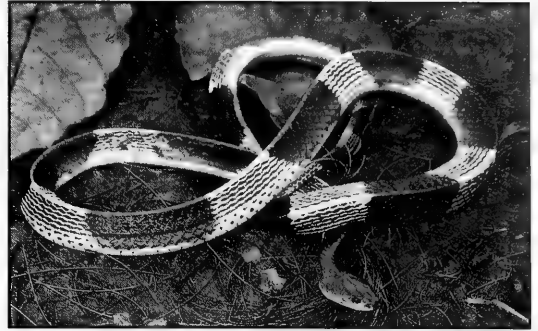
*Bungarus caeruleus magnimaculatus* Wall and Evans, 1901:611 (Type locality: Meiktila, Upper Burma; Holotype: BMNH 1908.6.23.90).

*Bungarus magnimaculatus*, Smith, 1943:417.— Toriba, 1993:120.— David and Ineich, 1999:69.

**DIAGNOSTIC CHARACTERS.**— Dorsal scales in 15 longitudinal rows at midbody; subcaudal scutes undivided throughout; middorsal row of scales (vertebrals) strongly enlarged, as broad as or broader than long; tail tapering, terminating in a point; ventrals 214–235; subcaudals 40–48. Dorsum with 11–14 broad, white crossbars, as wide as the black interspaces, the centers of each of the scales spotted with black; belly uniformly white. Total length 1300 mm; tail length 150 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 458): Magway, Mandalay, and Sagaing Divisions.

**HABITAT.**— An endemic to Myanmar, recent herpetological surveys have found this species primarily in indaing diptocarp forests (moist deciduous). The type locality of Meiktila, Upper Burma (referable to Mandalay Division), lies in seasonal dry forest; thus, this species is likely to occur throughout the central dry zone. Individuals have been located in disturbed habitats near villages and in agriculture areas. Active at night.



*Bungarus magnimaculatus*. Photo by Joseph B. Slowinski.

### *Bungarus wanghaotingi* Pope, 1928

*Bungarus multicinctus wanghaotingi* Pope, 1928:3 (Type locality: Yuankiang, Yunnan, China; Holotype: AMNH 35230).— Toriba, 1993:121.— David and Ineich, 1999:69.

*Bungarus multicinctus* (part) Smith, 1943:416.

**DIAGNOSTIC CHARACTERS.**— Dorsal scales in 15 longitudinal rows at midbody; subcaudal scutes undivided throughout; middorsal row of scales (vertebrals) strongly enlarged, as broad as or broader than long; tail tapering, terminating in a point; ventrals 209–228, subcaudals 44–54 (*vide* Pope 1935:339, Smith 1943:416). Belly uniformly white; dorsum with 20–31 light crossbands, crossbars narrower than black crossbars; 7–11 white crossbars on tail. Total length 1100 mm; tail length 145 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 458): Kachin State, Rakhine State, Sagaing Division, and Yangon area (doubtful). ELSEWHERE: China (Yunnan).

**HABITAT.**— This species has been found in a diverse set of habitats, from bamboo stands in coastal rainforest to streams in indaing forest (moist deciduous), to subtropical forests in Kachin State. Individuals have been encountered primarily in degraded habitats near villages and along roads. Wall (1926:564) noted that it has been found at low to mid-range elevations, at least up to about 900 m. A mating pair was found at night on 10 September in northern Kachin State. Active at dusk and at night.

**REMARKS.**— Closely related to but geographically distant from typical *B. multicinctus*. From *B. multicinctus*, it can be distinguished by the lower number of light cross bands on the body and tail (31–40 on the body and 9–17 on the tail in *B. multicinctus*, 20–31 and 7–11 respectively in *B. wanghaotingi*). The “*multicinctus-wanghaotingi*” species group requires study; it is likely polytypic and several closely related though distinct species likely are hidden presently under the names *multicinctus* and *wanghaotingi*.



*Bungarus wanghaotingi*. Photo by Hla Tun.

### Genus *Calliophis* Gray, 1834

*Calliophis* Gray, 1834, pl. 86, fig. 1 (Type species: *Calliophis gracilis* Gray, 1834).

*Maticora* Gray, 1834, pl. 86, fig. 2 (Type species: *Maticora lineata* Gray, 1834 [= *Aspis intestinalis* Laurenti, 1768]).— Slowinski, Boundy, and Lawson, 2001:239.

**REMARKS.**— Bourret (1935:414) lists “Burmanie” in his distribution statement for *Maticora bivirgata*, but Smith (1943:419) observed, “I do not know of any authentic records of the occurrence of this Malayan genus, now known as *Maticora*, within the area covered by this work.” Toriba (1993:151–152) also includes Myanmar in his range statement for *M. bivirgata* (and, as an aside, he places *C. maculiceps* in *Maticora*) but he, too, does not cite new evidence to justify its inclusion. Under the circumstances, we have chosen to remove *M. bivirgata* from the faunal list for Myanmar inasmuch as to date none have shown up in the survey collections that have been conducted during the past four years.

Regarding the status of the nominal genus *Maticora*, recent work has shown that the genus and its included species, *M. bivirgatus*, *M. intestinalis*, *M. maculiceps* (fide Toriba 1993), and *M. nigrescens*, are properly placed in the genus *Calliophis* (Slowinski, Boundy, and Lawson 2001).

### *Calliophis maculiceps* Günther, 1858

*Elaps maculiceps* Günther, 1858:232 (Type locality: East Indies; Holotype: BMNH 58.4.20.6).

*Callophis maculiceps*, Smith, 1943:420.

*Maticora maculiceps*, Toriba, 1993:153.— David and Ineich, 1999:128.

*Calliophis maculiceps*, Slowinski, Boundy, and Lawson, 2001:235–241.

**DIAGNOSTIC CHARACTERS.**— Body scales in 13 parallel longitudinal rows, not obliquely disposed; middorsal (vertebral) scales not enlarged; preocular in contact with nasal; ventrals: ♂ 174–186, ♀ 189–203; subcaudals: ♂ 25–31, ♀ 21–25; body above brown to reddish brown, with black spots, the latter arranged longitudinally along each side of the back; head and nape black with some yellow markings including a yellow spot on each side of the occiput; upper labials yellow; tail, below, pale blue or gray. Total length 1300 mm; tail length 150 mm.



*Calliophis maculiceps*. Photo by Hla Tun.

**DISTRIBUTION.**— MYANMAR (Map p. 459): as far north as 20°N. ELSEWHERE: Thailand, Cambodia, Laos, Malaysia.

**HABITAT.**— Cox et al. (1998) report this species from low elevation forests. The lone individual encountered during our recent surveys was found at night near a stream in a rubber and beetlenut plantation at an elevation of 43 m. The surrounding habitat is coastal rainforest and semi-evergreen forest. In Thailand, it is usually found under vegetation, rocks or logs (Cox 1991).

### Genus *Naja* Laurenti, 1768

*Naja* Laurenti, 1768 (Type species: *Naja lutescens* Laurenti, 1768 [= *Coluber naja* Linnaeus, 1758]).

### *Naja kaouthia* Lesson, 1831

*Naja kaouthia* Lesson, 1831:122 (Type locality: Bengal; Holotype: unknown).— Toriba, 1993:187.— David and Ineich, 1999:159.

*Naja naja kaouthia*, Smith, 1943:428, 431.

**DIAGNOSTIC CHARACTERS.**— Body scales smooth, arranged in 19–21 (usually 21) longitudinal rows at mid-body; throat pale, scarcely any dark mottling, often followed by a single dark band, ventrolateral throat spots distinct; remainder of venter either pale or increasingly cloudy with darker pigmentation towards the rear; in adults, hood markings usually distinct, usually a pale, oval or

circular marking, with a dark center (see fig., left image) and occasionally a narrow dark outer border; occasionally 1 or 2 dark spots are present in the pale oval; fangs not modified for spitting, venom discharge orifice large; ventrals 164–196; subcaudals 43–58. Total length 1500 mm; tail length 230 mm (according to Smith [1943:429] larger specimens have been recorded, but they are rare).

**DISTRIBUTION.**— MYANMAR (Map p. 459): widely distributed throughout the country in wetter habitats (Ayeyarwady Division, Chin State, Kachin State, Magway Division [part], Rakhine State, Sagaing Division [part], Yangon Division); in the drier central region, spanning Mandalay, Magway [part], and Sagaing [part] Divisions, it is replaced by *Naja mandalayensis* (q.v.). ELSEWHERE: Nepal, Bangladesh, northeastern India (Assam), Thailand (also in the wetter areas), northern Malaysia, Cambodia, southern Laos and southern Vietnam, southwestern China (Sichuan, Yunnan).

**HABITAT.**— Widely distributed in Myanmar except in the central dry zone (dry and moist deciduous forests) where its close relative, *N. mandalayensis*, occurs. *Naja kaouthia* is often encountered in villages, in agricultural areas, and grasslands, but it is also met with in primary coastal rainforest. It has also been encountered swimming in lakes and rivers, as well as beneath rocks and in the burrows of other animals. Additionally, Cox (1991) observes that it can climb trees. In Myanmar, it has been recorded from sea level to 820 m. Although most active at dusk and night, it may be encountered during the daylight hours as well.

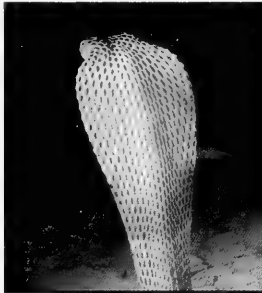
*Naja mandalayensis* Slowinski and Wüster, 2000

*Naja naja kaouthia*, Smith, 1943:431 (part).

*Naja mandalayensis* Slowinski and Wüster, 2000:257–270, figs. 1–2 (Type locality: near Monywa [22°13'N, 95°20'E], Sagaing Division, Myanmar; Holotype: CAS 207097).



*Naja kaouthia*. Photo by Hla Tun.



Hood markings in *Naja kaouthia* (left) and *Naja mandalayensis* (right). Photos by Dong Lin.



Underside of throat and anterior third of body color patterns for *Naja kaouthia* (left) and *Naja mandalayensis* (right). Photos by Dong Lin.

**DIAGNOSTIC CHARACTERS.**— Underside of chin and throat dark, set off from first dark band by 2 to 4 ventrals that are either pale or at least less densely mottled, followed by 2 or 3 broad dark bands, the remainder of the venter is pale with occasional dark mottling; hood without markings (see fig., right image) or, if present, scarcely discernible; fangs modified for spitting, venom discharge orifice small; ventrals: 173–185 (♂ 173–185, ♀ 182–185); subcaudals: 50–58 (♂ 56–58, ♀ 50–56). Total length 828 mm; tail length 152 mm (dimensions of holotype, a rather small specimen, as recorded by Slowinski and Wüster; larger individuals undoubtedly occur).

**DISTRIBUTION.**— MYANMAR (Map p. 459): Central dry zone, including parts of Sagaing, Mandalay, and Magway Divisions.

**HABITAT.**— This species appears to be restricted to the central dry zone. Most individuals have been found in the vicinity of villages and agricultural lands.

### Genus *Ophiophagus* Günther, 1864

*Ophiophagus* Günther, 1864 (Type species: *Hamadryas elaps* Günther, 1858 [= *Naja hannah* Cantor, 1836]).

#### *Ophiophagus hannah* (Cantor, 1836)

*Hamadryas hannah* Cantor, 1836:187 (Type locality: Sandarbans, near Calcutta, India; Holotype: Unknown).  
*Naja hannah*, Smith, 1943:436, fig. 140.

*Ophiophagus hannah*, Toriba, 1993:195.— David and Ineich, 1999:171.

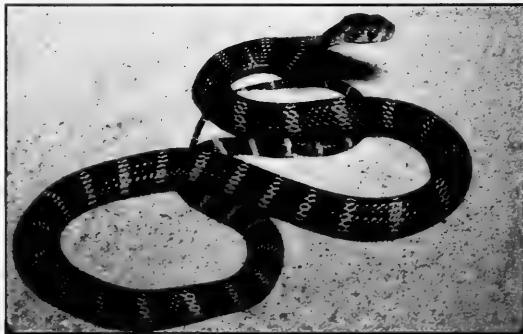
**DIAGNOSTIC CHARACTERS.**— Body scales smooth, obliquely arranged, in 17–19 rows on the neck, 15 at midbody; middorsal (vertebral) row and outer 2 lateral rows larger than others; ventrals 240–254; subcaudals 84–104, anterior scutes undivided; juveniles are usually dark brown or black with white or yellow cross bars, anteriorly the bars are chevron-shaped but straighten out posteriorly; with age, the light pattern disappears, and older adults are uniformly brown although some indication of the light cross bars persists (in Myanmar, the banded pattern persists in adults); tail dark olive to black. Total length recorded to 5500 mm, but individuals rarely exceed 4250 mm; tail length approximately 20% of total length.

**DISTRIBUTION.**— MYANMAR (Map p. 459): widely distributed (encountered by the Survey team on occasion at localities in both Ayeyarwady and Mandalay Divisions). ELSEWHERE: widely distributed throughout Southeast Asia and east to the Philippines and western Indonesia.

**HABITAT.**— In Myanmar, this species has been found in a variety of habitats, in dense forests, mangrove swamps, open country, and disturbed areas in the Ayeyarwady Delta, to the dry forests of the central dry zone to coastal rainforest in Tanintharyi. In Assam, Pawar and Birand (2001) confirm its presence in primary forest: in Thailand, Cox (1991) states that it is found in both forests



*Ophiophagus hannah* (adult). Photo by Hla Tun.



*Ophiophagus hannah* (juvenile). Photo by John Tashjian.

and plantations habitats; and in Peninsular Malaysia and Singapore, Lim and Lee (1989) note that it occurs in foothill jungles, open grasslands, in rural areas, and along jungle streams. David and Vogel (1996) state that in Sumatra it ranges from sea level to 1800 m.

### Genus *Sinomicrurus* Slowinski, Boundy, and Lawson, 2001

*Sinomicrurus* Slowinski, Boundy, and Lawson, 2001:239 (Type species: *Elaps macclellandii* Reinhardt, 1844).

#### *Sinomicrurus macclellandii* (Reinhardt, 1844)

*Elaps macclellandii* Reinhardt, 1844:532 (Type locality: Assam, India; Holotype: Unknown).

*Calliophis macclellandi*, Smith, 1943:423.

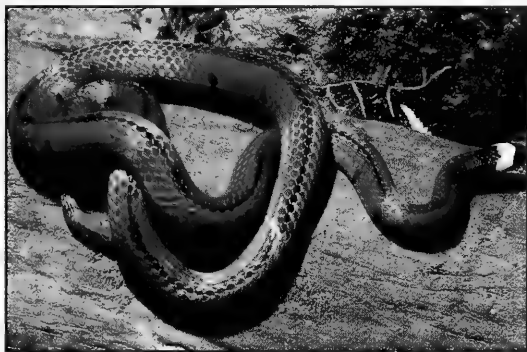
*Hemibungarus macclellandii*, David and Ineich, 1999:98.

*Hemibungarus macclellandii macclellandii*, Toriba, 1993:142.

*Sinomicrurus macclellandii*, Slowinski, Boundy, and Lawson, 2001:239.

*Sinomicrurus macclellandii macclellandii*, Hallermann et al., 2002:151.

**DIAGNOSTIC CHARACTERS.**— Vertebral series of scales not enlarged; body scales in 13 parallel longitudinal rows; 1 preocular; 2 postoculars; 7 upper labials; temporals 1 + 1, the anterior shield in contact with 2 upper labials; color pattern red or brownish above with a series of narrow black transverse bars (sometimes a narrow, black vertebral stripe with transverse black bars restricted to sides of body [Eastern Himalayas] or black transverse bars reduced to transverse vertebral spots [Assam, Upper Myanmar]) (*vide* Smith 1943:424); head black anteriorly reaching back to the level of the eyes, followed by a broad white band, which is bordered posteriorly by a black nuchal band; ventrals: ♂ 182–212, ♀ 208–244; subcaudals, mostly paired, occasionally a few single: ♂ 28–36, ♀ 25–33. Total length: ♂ 635 mm, ♀ 780 mm; tail length: ♂ 70 mm, ♀ 60 mm.



*Sinomicrurus macclellandii*. Photo by Nikolai Orlov.

**DISTRIBUTION.**— MYANMAR (Map p. 459): Kachin State south to (?) Yangon Division (based on questionable record). ELSEWHERE: India (Sikkim, Assam), Thailand, southern China, Vietnam.

**HABITAT.**— The only specimen of this species from recent surveys was found in the subtropical forests (Northern Triangle) of Kachin State at an elevation of 526 m during the day. Outside of Myanmar, this species has been recorded from elevations of 350 m to 2000 m (Schleich and Kästle 2002). According to Das (2002), it is generally nocturnal. Cox (1991) reports that in Thailand it is usually found under loose soil or vegetation in forests up to 1800 m.

### Subfamily HYDROPHIINAE

#### Genus *Laticauda* Laurenti, 1768

*Laticauda* Laurenti, 1768:109 (Type species: *Laticauda scutata* Laurenti, 1768).

#### *Laticauda colubrina* (Schneider, 1799)

*Hydrus colubrinus* Schneider, 1799:238 (Type locality: None specified; Holotype: ZMB 9078).

*Laticauda colubrina*, Smith, 1926:6; 1943:443.— Toriba, 1993:146.— David and Ineich, 1999:123.

**DIAGNOSTIC CHARACTERS.**— Ventrals large, one-third to more than half the width of the body;

nostrils lateral; nasals separated by internasals; 21–25 longitudinal rows of imbricate scales at midbody; an azygous prefrontal shield usually present; rostral undivided; ventrals 213–243; subcaudals: ♂ 37–47, ♀ 29–35 (ventral and subcaudal counts after Smith 1943:443). Upper lip yellow. Total length: ♂ 875 mm, ♀ 1420 mm; tail length: ♂ 130 mm, ♀ 145 mm.

**DISTRIBUTION.**—MYANMAR (Map p. 460): coastal waters, tidal rivers, and ashore especially along rocky coasts. According to Smith (1943:444), this species is not commonly met in “Indian and Indo-Chinese waters” though it is not uncommon at Singapore. Minton (1975:26, table 1) suggests that although rare in the Bay of Bengal, it may not be uncommon along the Myanmar coast and the west coast of the Malaysian peninsula. ELSEWHERE: coastal waters of Thailand, Malaysia, and western Indonesia as far east as Polynesia and north along the east Asian coast and Philippines Islands to southern Japan.

**HABITAT.**— Individuals of this species were found on a small, uninhabited island approximately one mile off the Rakhine coast in the Bay of Bengal. They were seen at rest during the day at low tide in rock crevices. Surrounding waters were rich in large corals. In New Caledonia, Ineich and Laboute (2002) report that it is often found inshore under vegetation. It has been found at depths of more than 60 m, but it appears to prefer depths of less than 20 m (Ineich and Laboute 2002). Active day and night (Ineich and Laboute 2002).

### *Laticauda laticaudata* (Linnaeus, 1758)

*Coluber laticaudatus* Linnaeus, 1758:222 (part) (Type locality: “in Indiis”; Holotype: NHRM 87–88).

*Laticauda laticaudata*, Smith, 1926:4; 1943:442.— Toriba, 1993:146.— David and Ineich, 1999:124.

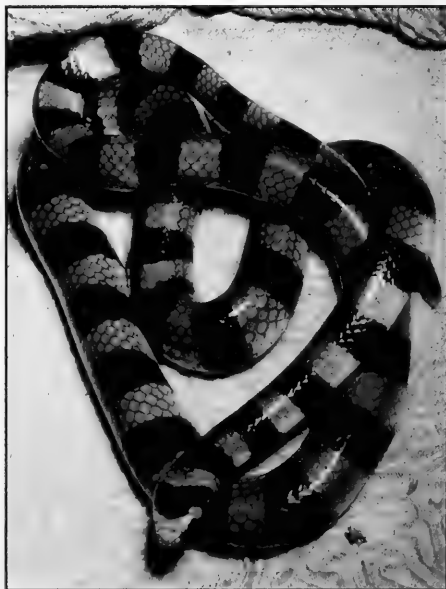
**DIAGNOSTIC CHARACTERS.**— Ventrals large, one-third to more than one half the width of the body; nostrils lateral; nasals separated by internasals; 19 longitudinal rows of imbricate scales at midbody; no azygous prefrontal shield; rostral undivided; ventrals 225–243; subcaudals: ♂ 38–47, ♀ 30–35 (ventral and subcaudal counts after Smith 1943:443). Upper lip dark brown. Total length: ♂ 910 mm, ♀ 1070 mm; tail length: ♂ 110 mm, ♀ 110 mm.

**DISTRIBUTION.**—MYANMAR (Map p. 460): Rakhine State. Smith (1943:443) states that it is “rare in the Oriental region (Calcutta and Little Nicobar Harbour).” On the other hand, Minton (1975:26, table 1) suggests that although rare in the Bay of Bengal, it may not be uncommon along the Myanmar coast and the west coast of the Malaysian peninsula. ELSEWHERE: western Indonesia (Sumatra and Java) to Australia, Melanesia and Polynesia, and north along the east coast of Asia to southern Japan.

**HABITAT.**— This species has been found near the



*Laticauda colubrina*. Photo by Dong Lin.



*Laticauda laticaudata*. Photo by John Tashjian.



mouth of a small freshwater stream along the Rakhine coast. The coast in this area is awash with exposed coral reef and mangrove forest. In Taiwan, Mao and Chen (1980) reported that it is often found near fresh water. Active day and night (Ineich and Laboute 2002).

### Genus *Disteira* Lacépède, 1804

*Disteira* Lacépède, 1804 (Type species: *Disteira doliata* Lacépède, 1804 [= *Hydrus major* Shaw, 1802]).

**REMARKS.**— At this time, we have chosen not to follow McDowell (1972) and continue to recognize the nominal genus *Enhydrina*, which he referred to the genus *Disteira*, and its included species, *E. schistosa*. We do so with some hesitation because we believe that McDowell was likely closer to the truth in synonymizing *Enhydrina* with *Disteira* and that the current arrangement merely perpetuates an unfortunate case of paraphyly. Pending further studies, however, we have chosen the conservative approach and follow McCarthy (1993) who recognizes the genus *Enhydrina* (q.v.) with its included species, *E. schistosa* and *E. zweifeli*.

### *Disteira nigrocincta* (Daudin, 1803)

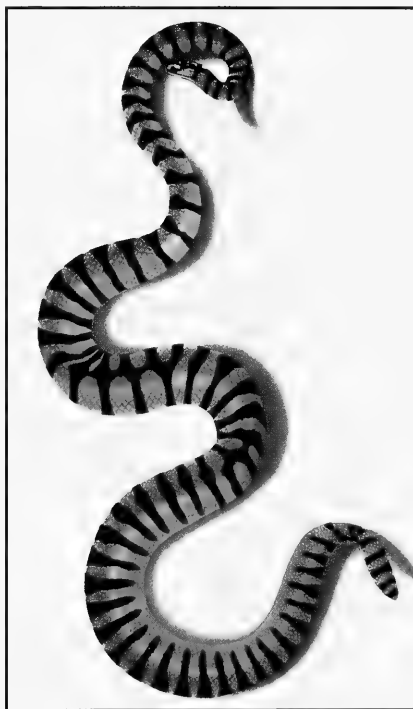
*Hydrophis nigrocinctus* Daudin, 1803:380 (Type locality: Sundarbans, Bengal; Holotype: BMNH 1946.1.10.13, but original description based on Russell, 1801, p. 7, pl. 6).— Smith, 1926:44, fig. 18; 1943:452.— David and Ineich, 1999:115.

*Disteira nigrocincta*, McDowell, 1972:239–244.— McCarthy, 1993:226.

**DIAGNOSTIC CHARACTERS.**— Mental scute large, not concealed in mental groove; 1–3 maxillary teeth behind fangs; 7–9 palatine teeth, similar in size to pterygoid teeth; head with yellow supraorbital stripe surrounding a blackish crown patch that extends forward to prefrontals; olive to brown above with 40 to 60 narrow dark annuli; yellowish below; 27–33 scale rows around neck, 39–45 around midbody, imbricate and keeled; ventrals 296–330, distinct throughout but not twice as large as adjacent scales; preanal scales enlarged. Total length 1080 mm, tail length 125 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters and tidal streams bordering the Bay of Bengal. ELSEWHERE: known only from the Bay of Bengal and adjacent coasts.

**HABITAT.**— Little is known about this species. Other members of this genus are diurnal and are found in deep, turbid, sandy bottom waters (O'Shea 1996).



*Disteira nigrocincta*. From Fayrer (1874, pl. 25).

### Genus *Enhydrina* Gray, 1849

*Enhydrina* Gray, 1849:47 (Type species: *Enhydrina valakadyen* Gray, 1849 [= *Hydrus valakadyen* F. Boie, 1827 = *Hydrophis schistosus* Daudin, 1803]).

Remarks: See note above under the genus *Disteira*.

***Enhydrina schistosa* (Daudin, 1803)**

*Hydrophis schistosus* Daudin, 1803:386 (Type locality: Tranquebar, South India; Holotype: BMNH 1946.1.10.7, but original description based on Russell, 1801, pl. 10).

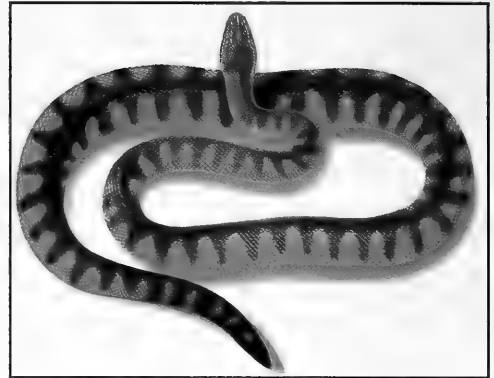
*Enhydrina schistosa*, Smith, 1926:36, fig. 17; 1943:449, fig. 144.— McCarthy, 1993:227.— David and Ineich, 1999:92.

*Disteira schistosa*, McDowell, 1972:239–244.

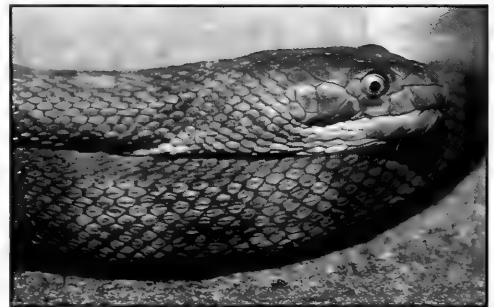
**DIAGNOSTIC CHARACTERS.**— Mental scute small, partly concealed within mental groove; 3–4 maxillary teeth behind fangs; 5–6 palatine teeth, palatine teeth larger than pterygoid teeth; no suborbital stripe; young dark gray above, whitish below, with dark gray or black annuli; pattern disappears in adults which are uniform gray in color; scales around body variable, in Bay of Bengal, scales around neck, males 43–52, females 48–55, scales around midbody, ♂ 53–60, ♀ 55–65, scales somewhat imbricate or juxtaposed, with short central keel; ventrals 262–322; preanal scales only slightly enlarged. Total length 1400 mm, tail length 180 mm (but rarely exceeding 1100 mm total length).

**DISTRIBUTION.**— MYANMAR (Map p. 460): coastal waters (two specimens, one in the Myanmar Biodiversity Museum, the second at the California Academy of Sciences come from Ayeyarwady Division coastal waters). ELSEWHERE: coastal waters from the Persian Gulf east to Indonesia, New Guinea and northern Australia, and north from Malaysia to the Philippines.

**HABITAT.**— According to Cogger (1975), in Australia this species is often found in rivers, but it is not clear if they are found in the brackish waters of the tidal basins or further away from the estuaries upstream in freshwater. Cox et al. (1998) likewise report that in Thailand *E. schistosa* is sometimes found in estuaries and rivers as well as coastal waters, but again it is not clear how far upstream they go. According to O'Shea (1996), this species prefers water of depths from less than 5 m to a maximum of around 30 m. The individuals encountered in our recent surveys were caught in nets at the mouth of a river. Active during day and night (O'Shea 1996).



*Enhydrina schistosa*. From Fayrer (1874, pl. 18).



*Enhydrina schistosa*. Photo courtesy Indraneil Das.

**Genus *Hydrophis* Latrielle, 1802**

*Hydrophis* Latrielle, 1802:193 (Type species: *Hydrus fasciatus* Schneider, 1799).— Smith, 1926:40; 1943:451.— McCarthy, 1993:229.

***Hydrophis atriceps* Günther, 1864**

*Hydrophis atriceps* Günther, 1864:371, fig. (Type locality: Siam; Syntypes: BMNH 1946.1.2.62, 63.9.29.5).— McCarthy, 1993:230.— David and Ineich, 1999:104.

*Hydrophis fasciatus atriceps*, Smith, 1926:97, fig. 27; 1943:465.

**DIAGNOSTIC CHARACTERS.**— Head small, body long and slender anteriorly; scales on thickest part of body subquadrangular or hexagonal in shape, juxtaposed or slightly imbricate; 5–6 maxillary teeth behind fangs; 2 anterior temporals; body scales in 25–30 (usually 27–29) rows around the neck, 39–49 (usually 43–45) around midbody (increase in number of rows from neck to midbody 12–21, usually 14–18); ventral scales 323–452 (average 366 or less); anterior part of body including head and neck dark olive to black with pale oval yellowish spots on sides, sometimes connected as crossbars; posterior, grayish; below whitish; dark rhomboidal spots may extend down the sides of the body and form complete annuli in young. Total length ♂ 1100 mm, ♀ 990 mm; tail length ♂ 100 mm, ♀ 75 mm.

**DISTRIBUTION.**— MYANMAR (*fide* Toriba 1993), but according to Smith (1943:465), *H. atriceps* occurs from the Gulf of Siam eastward and is not known to the west. David and Ineich (1999:105) do not include Myanmar in its recorded range. All references to *H. atriceps* from the Bay of Bengal are most probably *H. fasciatus*, with which *H. atriceps* has long been associated.

**HABITAT.**— Smith (1926) reports this species to be common at the mouths of rivers.

**REMARKS.**— This species is so similar in appearance to *H. flaviceps* that the two have been regarded as conspecific, though treated as distinct subspecies (Smith 1926:97 and 1943:465). The differences between them are given in the diagnoses. *Hydrophis atriceps* should be removed from the Myanmar faunal list.

### *Hydrophis caeruleus* (Shaw, 1802)

*Hydrus caeruleus* Shaw, 1802:561 (Type locality: Indian Ocean [Vizagapatam {=Visakhapatnam}]); Holotype: BMNH 1946.1.3.90).

*Hydrophis caeruleus*, Smith, 1926:90; 1943:463.— McCarthy, 1993:232.— David and Ineich, 1999:106.

**DIAGNOSTIC CHARACTERS.**— Scales on thickest part of body quadrangular or hexagonal in shape, feebly imbricate or juxtaposed; 14–18 maxillary teeth behind front fangs; 2 anterior temporals; scales in 31–43 rows on the neck, 38–54 around midbody (increase from neck to midbody 6–14); ventrals 253–334, distinct throughout though not twice as large as adjacent body scales; bluish gray above, whitish below, with 40–60 broad bands, about twice as wide as interspaces, tapering ventrally (in older adults, bands become indistinct).

**DISTRIBUTION.**— MYANMAR: coastal waters, especially abundant in the Mergui Archipelago (Tanintharyi Division). ELSEWHERE: both west and east coasts of India (vicinity of Bombay and Karwar in the west and from Madras to the mouth of the Ganges on the east coast) east through Straits of Malacca to the Gulf of Siam to southeastern China and western Indonesia.

**HABITAT.**— No data available.

### *Hydrophis cantor* Günther, 1864

*Hydrophis cantor* Günther, 1864:374, fig. (Type locality: Penang, Malaysia; Holotype: BMNH 1946.1.18.30)— McCarthy, 1993:232.— David and Ineich, 1999:106.

*Microcephalophis cantor*, Smith, 1926:124, fig. 35; 1943:475.

**DIAGNOSTIC CHARACTERS.**— Head small, body long and slender anteriorly; scales on thickest part of body juxtaposed; 5–6 maxillary teeth behind fangs; 23–25 (rarely 21) scale rows around neck, 41–48 around thickest part of body (increase from neck to midbody 18–24); ventrals divided by a longitudinal fissure; prefrontal in contact with third upper labial; ventrals 404–468. Total length ♂ 1450 mm, ♀ 1880 mm; tail length ♂ 120 mm, ♀ 140 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters. ELSEWHERE: coastal waters from Pakistan (Karachi) east, including India, Sri Lanka, Thailand and Malaysia.

**HABITAT.**— No data available.

***Hydrophis fasciatus* (Schneider, 1799)**

*Hydrus fasciatus* Schneider, 1799:240 (Type locality: East Indies; Syntypes: ZMB 2836–2837).

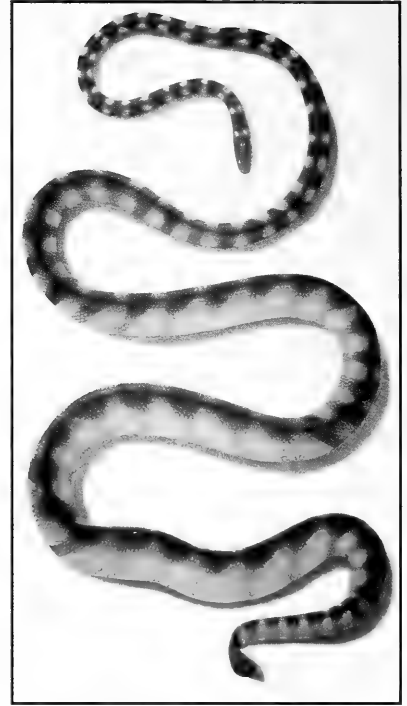
*Hydrophis fasciatus*, Smith 1926:94; 1943:464.— McCarthy, 1993:234.— David and Ineich, 1999:109.

**DIAGNOSTIC CHARACTERS.**— Head small, body long and slender anteriorly; scales on thickest part of body subquadrangular or hexagonal in shape, juxtaposed or slightly imbricate; 5–6 maxillary teeth behind fangs; 2 anterior temporals; body scales in 28–33 rows around the neck, 47–58 around midbody (increase in number of rows from neck to midbody 20–27); ventral scales 414–514 (average 460); anterior part of body including head and neck dark olive to black with pale oval yellowish spots on sides, sometimes connected as crossbars; posterior, grayish; below whitish; dark rhomboidal spots may extend down the sides of the body and form complete annuli in young. Total length ♂ 1100 mm, ♀ 990 mm; tail length ♂ 100 mm, ♀ 75 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters to the Straits of Malacca. ELSEWHERE: common along east coast of India (said to be rare along the west coast but it has been reported from as far west as Karachi).

**HABITAT.**— Cox et al (1998) report this nocturnal species inhabits shallow coastal waters.

**REMARKS.**— So similar in appearance to *H. atriceps* that the two have been regarded as conspecific, though treated as distinct subspecies (see Smith 1926:97 and 1943:465) (see also above, Remarks, under *H. atriceps*).



*Hydrophis fasciatus*. From Fayrer (1874, pl. 27).

***Hydrophis gracilis* (Shaw, 1802)**

*Hydrus gracilis* Shaw, 1802:560 (Type locality: Unknown; Holotype: BMNH 1946.1.17.37).

*Microcephalophis gracilis*, Smith, 1926:121; 1943:472, fig. 150.

*Hydrophis gracilis*, McCarthy, 1993:234.— David and Ineich, 1999:110.

**DIAGNOSTIC CHARACTERS.**— Head small, body long and slender anteriorly; scales on thickest part of body juxtaposed; 5–6 maxillary teeth behind fangs; 17–21 scale rows around neck, 30–36 around thickest part of body (increase from neck to midbody 18–24); ventrals divided by a longitudinal fissure; prefrontal in contact with third upper labial; ventrals 220–287. Total length ♂ 950 mm, ♀ 1025 mm; tail length ♂ 80 mm, ♀ 95 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters. ELSEWHERE: coastal waters from the Persian Gulf east to India, Sri Lanka, Thailand, Malaysia, Vietnam, China, Taiwan, Indonesia (Sumatra and Java), Australia, Melanesia.

**HABITAT.**— Reported to inhabit deep turbid offshore waters (O'Shea 1996).

**REMARKS.**— Smith (1943:473) provides information on the geographic variation in scale counts for this species. The values included in the diagnosis above apply only to those populations inhabiting the coastal waters of Myanmar and along the east coast of India.

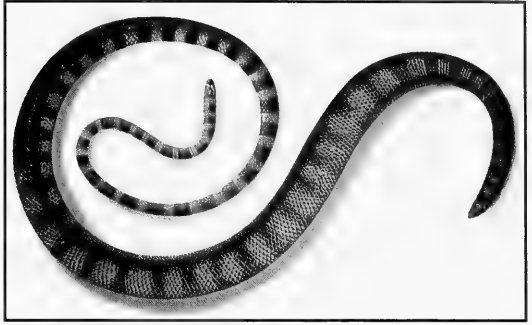
*Hydrophis obscurus* Daudin, 1803

*Hydrophis obscurus* Daudin, 1803:375 (Type locality: Sandbarbans [*sic*], India; Holotype: BMNH 1946.1.9.27 [but original description based on Russell, 1801, pl. 8]).— Smith, 1926:66; 1943:457.— McCarthy, 1993:238.— David and Ineich, 1999:115.

**DIAGNOSTIC CHARACTERS.**— Scales on thickest part of body with rounded or bluntly pointed tips, imbricate throughout; 5–7 maxillary teeth behind fangs; body elongate, ventrals distinct throughout, 300–338; 6–7 upper labials; 1 anterior temporal; 19–23 scale rows on neck, 29–37 on thickest part of body (increase from neck to midbody 8–14); young black with 35–55 bright yellow or whitish dorsal bars, posteriorly becoming complete bands that encircle body, head with curved yellow marking extending from snout to either side of parietal scales; adults markings become indistinct and older individuals almost uniform grayish above, yellowish below. Total length ♂ 1190 mm, ♀ 1200 mm; tail length ♂ 135 mm, ♀ 110 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters especially of the Ayeyarwady Division and south (Tanintharyi Division). ELSEWHERE: east coast of India.

**HABITAT.**— This species is reported to occur mainly in brackish waters (Smith 1926), and historical records indicate that it can be found at the mouths of rivers (*ibid.*).



*Hydrophis obscurus*. From Fayrer (1874, pl. 26).

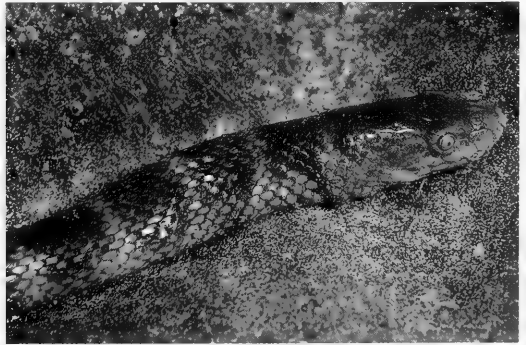
*Hydrophis ornatus* (Gray, 1842)

*Aturia ornata* Gray, 1842:61 (Type locality: Indian Ocean; Holotype: BMNH 1946.1.23.72).

*Hydrophis ornatus*, Smith, 1926:6.— David and Ineich, 1999:116.

*Hydrophis ornatus ornatus*, Smith, 1943:460.— McCarthy, 1993:239.

**DIAGNOSTIC CHARACTERS.**— Scales on thickest part of body more or less hexagonal in shape, feebly imbricate or juxtaposed; 10–13 maxillary teeth behind fangs; head large; body robust, not elongate, greatest diameter posteriorly about twice that of the neck; 1 preocular; 2 postoculars; 2 anterior temporals; 7–8 upper labials; scale rows on neck: ♂ 28–37, ♀ 31–45, on thickest part of body, ♂ 33–45, ♀ 39–55 (increase from neck to midbody 4–12); ventrals distinct throughout, in ♂ 209–260, in ♀ 236–312, anteriorly ventrals about twice as large as adjacent scales, narrowing posteriorly; above grayish or light olive to almost white with broad dark bars or rhomboidal spots sep-



*Hydrophis ornatus*. Photos by Dong Lin.

arated by narrow interspaces; below yellowish or whitish. Total length ♂ 950 mm, ♀ 860; tail length ♂ 115 mm, ♀ 80 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 460): coastal waters. ELSEWHERE: widely distributed from the Persian Gulf east to New Guinea and Australia and north along the coast of China to the Ryukyu Archipelago.

**HABITAT.**— Reported to inhabit clear waters with coral reefs, as well as turbid rivers and estuaries (O'Shea 1996; Ineich and Laboute 2002). Active at night and day (Ineich and Laboute 2002).

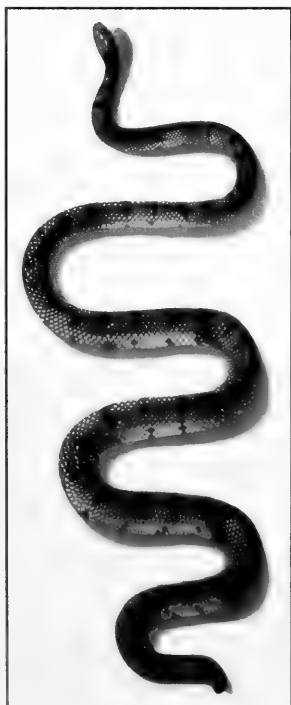
**REMARKS.**— Smith (1943:461) recognized two subspecies, *H. o. ornatus* and *H. o. ocellatus*, the latter in the coastal waters of Australia. In 1993, McCarthy synonymized *H. o. ocellata* with *H. o. ornatus* but recognized *H. o. maresinensis*, described by Mittleman in 1947 to accommodate the populations found off the coast of China, Taiwan and the RyuKyu Islands.

### *Hydrophis spiralis* (Shaw, 1802)

*Hydrus spiralis* Shaw, 1802:564 (Type locality: Indian Ocean; Holotype: BMNH 1946.1.6.94).

*Hydrophis spiralis*, Smith, 1926:48; 1943:453.— McCarthy, 1993:240.— David and Ineich, 1999:118.

**DIAGNOSTIC CHARACTERS.**— Scales on thickest part of body with rounded or pointed tips, imbricate; 6–7 maxillary teeth behind fangs; normally 1 anterior temporal; 6–8 upper labials; 25–31 scale rows around neck, 33–38 around midbody (increase from neck to midbody 4–8); ventrals 295–362, distinct throughout, about twice as broad as adjacent body scales; yellowish or yellowish-green above, dorsal scales edged with black, 41–46 narrow black bands encircle body, the bands usually less than one-third the width of the lighter interspaces; head in young black with yellow horseshoe-shaped marking, in adult head usually yellow. Total length ♂ 1620 mm, ♀ 1830 mm; tail length ♂ 140 mm, ♀ 120 mm.



*Hydrophis spiralis*  
From Fayrer (1874, pl. 21).

*Hydrophis stricticollis*  
From Fayrer (1874, pl. 28).



**DISTRIBUTION.**— MYANMAR: coastal waters and tidal rivers. ELSEWHERE: Persian Gulf east to central Indonesia (Sulawesi) and north to the Philippines.

**HABITAT.**— Little is known about the natural history of this species; it has been reported in deep water habitats (Ineich and Laboute 2002).

***Hydrophis stricticollis* Günther, 1864**

*Hydrophis stricticollis* Günther, 1864:376, fig. (Type locality: India; Holotype: BMNH 1946.1.6.90).— Smith, 1926:73; 1943:459.— McCarthy, 1993:241.— David and Ineich, 1999:119.

**DIAGNOSTIC CHARACTERS.**— Scales on thickest part of body subquadrangular or hexagonal in shape, feebly imbricate or juxtaposed; 8–11 maxillary teeth behind fangs; head small, body long and slender anteriorly, posteriorly 2.5 to 3 times thicker than anteriorly; 1 anterior temporal, rarely divided; 7–8 upper labials, second in contact with prefrontal, 3–4 border eye; 34–41 scale rows around neck, 45–55 around midbody; ventrals 374–452, distinct throughout, less than twice as large as adjacent body scales; grayish to olive above, yellowish below, with 45–65 dark bands, widest dorsally, disappearing with age; head black or olive, yellow markings on snout and along sides of head. Total length ♂ 1050 mm, ♀ 1050 mm; tail length ♂ 140 mm, ♀ 90 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters from Rakhine State south to Gulf of Martaban. ELSEWHERE: east coast of India from Orissa to Bengal, and Bangladesh.

**HABITAT.**— Historic records exist for this species in rivers in the Bago Division (Smith 1926); however, not much is known about its habitat preferences.

**Genus *Kerilia* Gray, 1849**

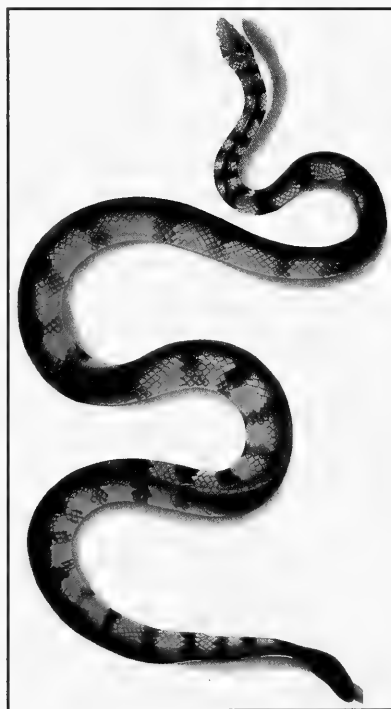
*Kerilia* Gray, 1849:57 (Type species: *Kerilia jerdoni* Gray, 1849).— Smith, 1926:31; 1943:446.

***Kerilia jerdoni* Gray, 1849**

*Kerilia jerdoni* Gray, 1849:57 (Type locality: Madras, India; Holotype: BMNH III.8.1.a).— Smith, 1926:31, fig. 15; 1943: 447, fig. 143.— McCarthy, 1993:242.— David and Ineich, 1999:120.

**DIAGNOSTIC CHARACTERS.**— Body subcylindrical, nearly uniform diameter throughout; scales keeled and imbricate, in 17–23 longitudinal rows, 17 on neck, 21–23 (19–21 for the Bay of Bengal) at midbody; head short; prefrontals usually not in contact with upper labials; 6 upper labials, 3–4 bordering eye; 1 pre- and 1 postocular; 1 large anterior temporal; ventrals 225–253 for the Bay of Bengal and Gulf of Siam (247–278 further east), small, distinct throughout, usually entire; olive above, yellowish or white below, with black dorsal spots of crossbars that form complete bands, especially in young. Total length 1000 mm, tail length 100 mm.

**DISTRIBUTION.**— MYANMAR: Tanintharyi Division (Mergui Archipelago). ELSEWHERE: east coast of India and Sri Lanka east to the Straits of Malacca, the east coast of Malaysia to Borneo.



*Kerilia jerdoni*. From Fayrer (1874, pl. 20).



**Genus *Lapemis* Gray in Hardwicke and Gray, 1834**

*Lapemis* Gray in Hardwicke and Gray, 1834, vol. 2, pl. 87, fig. 2 (Type species; *Lapemis hardwickii* Gray).

**REMARKS.**— McDowell (1972) argued that he could not distinguish the genus *Thalassophina* Smith (1926) (type species, *Thalassophis viperina* Schmidt [1852]) from *Lapemis*. Although we believe that McDowell's views deserve serious consideration, again, as with *Enhydrina* (q.v.), we have taken the conservative approach and recognize *Thalassophina* as a distinct genus.

***Lapemis hardwickii* Gray in Hardwicke and Gray, 1834**

*Lapemis hardwickii* Gray in Hardwicke and Gray, 1834, vol. 2, pl. 87 (Type locality: Penang, Malaysia;

Holotype: BMNH 1946.1.18.39).— Smith, 1926:108, fig. 32, pl. 1, fig. 3; 1943:468, figs. 148–149.

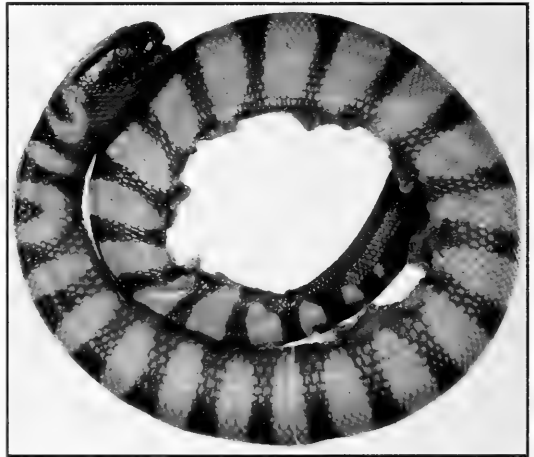
*Lapemis curtis hardwickii*, McCarthy, 1993:244.

**DIAGNOSTIC CHARACTERS.**— Body short, stout, neck region not less than half as thick at midbody; head large; scales squarish or hexagonal, juxtaposed, outer 3–4 rows larger than others, scale rows: ♂ 23–31 around neck, ♀ 27–35, around midbody, ♂ 25–27, ♀ 33–41; ventrals small, usually distinct anteriorly, not so posteriorly, in ♂ 114–186, in ♀ 141–230; head shields entire, parietals occasionally divided; nostrils superior, nasals in contact with one another; prefrontal usually in contact with second upper labial; 7–8 upper labials, 3–4 bordering eye; 1 pre- and 1–2 postoculars; 2, rarely 3, anterior temporals; greenish or yellow-olive above, whitish below, 35–50 olive to dark gray dorsal bars, tapering to a point laterally, occasionally encircling body, a narrow dark ventral stripe or broad irregular band occasionally present; adults often lack any pattern and are uniform olive to dark gray; head pale olive to black, yellow markings on snout present or not. Total length 860 mm, tail length 85 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 460): coastal waters of the Tanintharyi Division (Mergui Archipelago). ELSEWHERE: southeast coast of India and the Straits of Malacca, east to Australia and north to China, Philippines, Taiwan, and Japan.

**HABITAT.**— Known to be active during both day and night, this species is found to inhabit coral reefs; it also occurs in estuaries, and tidal zone regions with sandy or muddy bottoms (O'Shea 1996). It is usually found at depths of 6 to 15 m, but it has been encountered in deeper waters (O'Shea 1996).

**REMARKS.**— Gritis and Voris (1990) do not recognize *L. hardwickii* as a distinct species, placing it in the synonymy of *L. curtis*. McCarthy (1993) recognizes it as a subspecies of *L. curtis*, allowing that the nominate form inhabits coastal waters from the Persian Gulf to the shores of western India, and *L. curtis hardwickii* ranges from the coastal waters of Sri Lanka and eastern India east to New Guinea and Australia and north to the coast of China, the Philippines, and Japan (see also David and Ineich 1999:121–122). Smith (1926:113, 1943:471) argues that *L. curtis* ranges from the Persian Gulf to the west coast of India as far as Sri Lanka but that it is unknown along the east coast of India. We have chosen to follow Smith's treatment of the two and recognize *L. hardwickii* as a distinct species.



*Lapemis hardwickii*. (A preserved specimen; CAS-SU 12434.)

### Genus *Pelamis* Daudin, 1803

*Pelamis* Daudin, 1803:361 (Type species: *Pelamis bicolor* Schneider, 1799 [= *Anguis platura* Linnaeus, 1766]).

### *Pelamis platurus* (Linnaeus, 1758)

*Anguis platura* Linnaeus, 1766:391 (Type locality: Unknown; Holotype: Unknown).

*Pelamis platurus*, Smith, 1926:116, fig. 33; 1943:476.— McCarthy, 1993:245.— David and Ineich, 1999:174.

**DIAGNOSTIC CHARACTERS.**— Body compressed, posteriorly more than twice the diameter of the neck; body scales juxtaposed, subquadrangular in shape, in 49–67 rows around thickest part of body; ventral scales, 264–406, very small and, if distinct, divided by a longitudinal groove, but usually indistinguishable from adjacent body scales; head narrow, snout elongate, head shields entire, nostrils superior, nasal shields in contact with one another; prefrontal in contact with second upper labial; 1–2 pre- and 2–3 postoculars; 2–3 small anterior temporals; 7–8 upper labials, 4–5 below eye but separated from border by subocular; color variable but most often distinctly bicolored, black above, yellow or brown below, the dorsal and ventral colors sharply demarcated from one another; ventrally there may be a series of black spots or bars on the yellow or brown background, or the yellow may extend dorsally so that there is only a narrow middorsal black stripe, or a series of black crossbars (see Smith 1943:476–477 for a more complete description of the color pattern variants). Total length ♂ 720 mm, ♀ 880 mm; tail length ♂ 80 mm, ♀ 90 mm.



*Pelamis platurus*. Photo by John Tashjian.

**DISTRIBUTION.**— The most widely distributed of all sea snakes ranging from the east coast of Africa throughout southern and eastern coastal Asia, as far north as southern Siberia, east throughout Indonesia to Australia and Tasmania. It is also known from the Gulf of Panama and north to Baja California in western North America, having arrived there probably during the interstadial, warm periods of the Pleistocene via a circum-Alaska route following the Japanese and California currents. Occasional strays have shown up in the Galapagos Archipelago to the south and in the Hawaiian Islands.

**HABITAT.**— Although primarily a pelagic species, it has also been found in bays and estuaries. Active during the day and night (O'Shea 1996).

### Genus *Thalassophina* Smith 1926

*Thalassophina* Smith, 1926:33 (Type species: *Thalassophis viperina* Schmidt 1852).

**REMARKS.**— The correct name for this genus has been the subject of controversy for some years. Most recently, David and Ineich (1999:177) have argued that *Praescutata* is the proper name to use. The question arises because of uncertainty of just when the errata notice that accompanies Wall's original description of the genus was inserted into his publication, before or after distribution had begun. If before, then the work was "published" with the errata sheet, which becomes part of the original publication; if after some copies had been distributed, then David and Ineich's interpretation is justified. David and Ineich state that Wall's errata "was obviously written after the main part of the work, and later inserted in distributed copies." The question is not in when the errata

sheet was written or even printed, but when it was published, that is available for distribution. For the present, we choose to recognize *Thalassophina* as the valid name for the genus.

***Thalassophina viperina* (P. Schmidt, 1852)**

*Thalassophis viperina* Schmidt, 1852:79, pl. 3 (Type locality: Java; Holotype: ZMH 404).

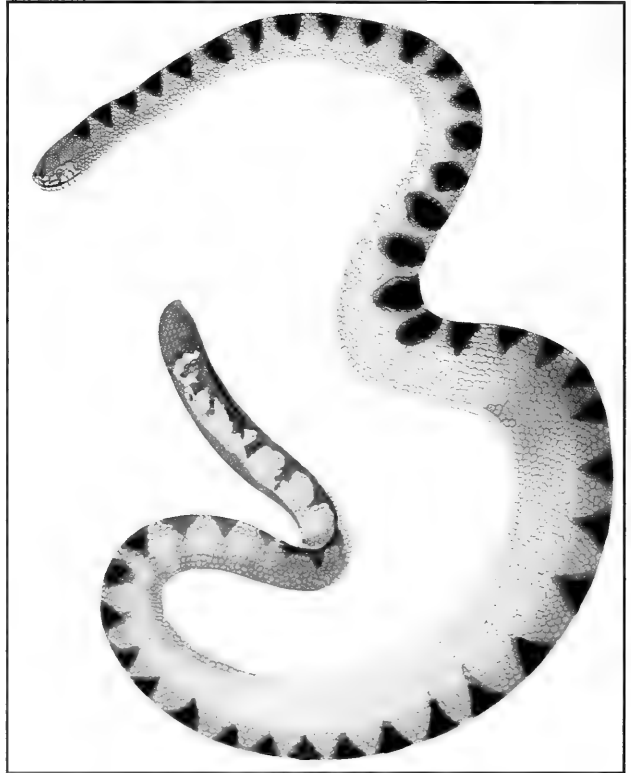
*Thalassophina viperina*, Smith, 1926:33, fig. 16.— McCarthy, 1993:247.

*Praescutata viperina*, Smith, 1943:448.— David and Ineich, 1999:177.

**DIAGNOSTIC CHARACTERS.**—

Scales hexagonal, juxtaposed, in 27–34 rows on the neck, 37–50 at midbody; ventrals 226–274, anteriorly about half the width of the body, narrowing posterior to about twice the width of the adjacent scales, or slightly less; head shields entire, nostrils superior, nasal shields in contact with one another; prefrontals longer than broad, not in contact with upper labials; 1, rarely 2, pre- and 1–2 postoculars; 7–9 upper labials, 3–5 bordering eye (sometimes only 3–4 or 4–5); usually 1 anterior temporal, occasionally 2 or 3; body color, more or less bicolored, gray above, white below, the 2 usually clearly demarked on the sides, often with 25–35 dark rhomboidal spots, rarely with dark bands. Total length ♂ 925 mm, ♀ 820 mm; tail length ♂ 100 mm, ♀ 80 mm.

**DISTRIBUTION.**— MYANMAR: coastal waters. ELSEWHERE: Persian Gulf east to Gulf of Siam, southern China and Borneo.



*Thalassophina viperina*. From P. Schmidt, 1852, pl. 3.

**FAMILY VIPERIDAE**

**Subfamily AZEMIOPINAE**

**Genus *Azemiops* Boulenger, 1888**

*Azemiops* Boulenger, 1888 (Type species: *Azemiops feae* Boulenger, 1888).

***Azemiops feae* Boulenger, 1888**

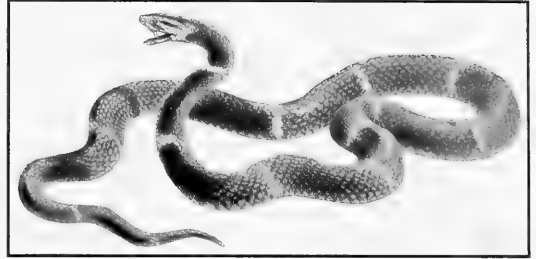
*Azemiops feae* Boulenger, 1888:603, pl. 7 (Type locality: Kakhyen Hills, Burma; Holotype: MSNM 30891).— Smith, 1943:480, fig. 152.— Toriba, 1993:258.— Zhao and Adler, 1993:274.— David and Ineich, 1999:205— McDiarmid, Campbell, and Touré, 1999:230.— Mallow, Ludwig, and Nilson, 2003:14, pl. 1.1

**DIAGNOSTIC CHARACTERS.**— No sensory pit between nostril and eye; body cylindrical; head

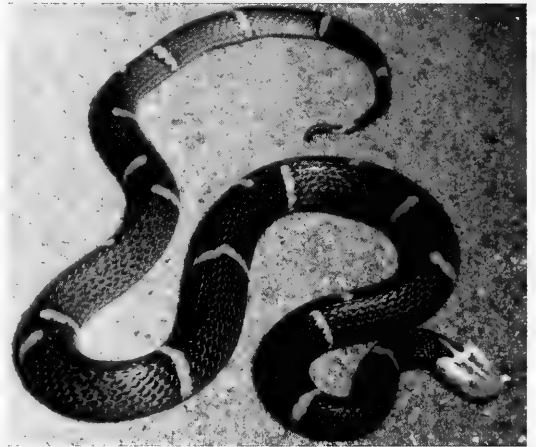
flattened, above covered with large, symmetrical shields; nostril large, in single completely differentiated nasal; loreal shield present, small; 2 pre- and 2 postoculars; eye with vertically elliptic pupil; scales smooth, in 17 longitudinal rows at midbody; ventrals 180–189; subcaudals 42–53, mostly paired, occasionally anterior shields undivided; blackish above, scales often edged with gray, 14–15 narrow white or pinkish crossbands, sometimes interrupted middorsally, or alternating with one another laterally; head yellow with a pair of dark brown to black stripes of somewhat irregular width extending from prefrontals to the black color on the neck. Total length ♂ 925 mm, ♀ 820; tail length ♂ 100 mm, ♀ 80 mm.

**DISTRIBUTION.**— MYANMAR: Kachin State. ELSEWHERE: southern and central China (western Yunnan and Shaanxi east to Zhejiang and south to Guangxi), and northern Vietnam.

**HABITAT.**— Although little is known about the natural history of this species, Kardong (1986) (summarizing Zhao and Zhao 1981) reports that it inhabits mountainous terrain at elevations between 1000–2000 m, but it has also been found in degraded habitats such as paddy, grassy fields and in and about villages. Historical records of this species in Myanmar indicate that it occurs in the Northern Triangle subtropical forest and the Nujiang Langcang Gorge's alpine-conifer and mixed-deciduous forest. For additional comments see Mallow et al. (2003).



*Azemiops feae*. From Boulenger, 1888, pl. 7.



*Azemiops feae*. Photo by John Tashjian.

### Subfamily VIPERINAE

#### Genus *Daboia* Gray, 1842

*Daboia* Gray, 1842:69 (Type species: *Daboia elegans* Gray, 1842 [= *Vipera daboia* Daudin, 1803=*Coluber russelii* Shaw and Nodder, 1797], *vide* Smith, 1943:482).

#### *Daboia russelii* (Shaw and Nodder, 1797)

*Coluber russelii* Shaw and Nodder, 1797:291 (Type locality: India; Holotype: BMNH I.I.I.a).

*Vipera russelli siamensis*, Smith, 1917:223; 1943:484, fig. 153.

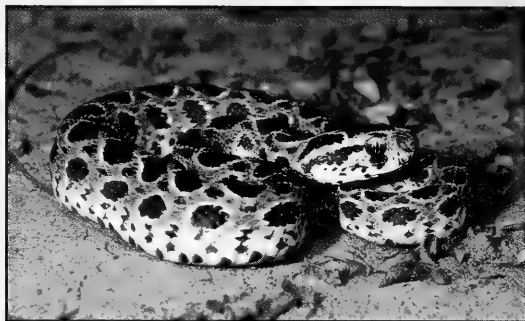
*Daboia russelli siamensis*, Toriba, 1993:268.

*Vipera russellii*, Zhao and Adler, 1993:278.

*Daboia russelii*, David and Ineich, 1999:312.— McDiarmid, Campbell, and Touré, 1999:371.— Mallow, Ludwig, and Nilson, 2003:150, pl. 7.2.

**DIAGNOSTIC CHARACTERS.**— No sensory pit between nostril and eye; head very distinct from neck, above covered by small, keeled, imbricate scales, 6–9 between narrow supraoculars; nostril large, in large nasal shield which, below, is fused to the rostral; eye, with vertically elliptic pupil, surrounded by 10–15 small scales, 3–4 rows of small scales separating the circumocular scales from the upper labials; temporals small; 10–12 upper labials; 27–33 longitudinal rows of scales at

midbody, all except outmost row strongly keeled; ventrals 153–180; subcaudals 41–64, all paired; color above light brown with 3 longitudinal series of large black-margined brown spots or blotches, the vertebral series often merging to form a chain-like longitudinal stripe, occasionally an additional longitudinal series of small dark spots between vertebral and lateral series; yellowish white below occasionally with dark brown markings. Total length to 1600 mm are not uncommon (*fide* Smith 1943:484).



*Daboia russelii*. Photo by Hla Tun.

**DISTRIBUTION.**—MYANMAR (Map p. 461): Ayeyarwady Division, Bago Division, Magway Division, Mandalay Division, Sagaing Division, Shan State, Yangon Division. ELSEWHERE: southern China, Taiwan, India, Pakistan, Sri Lanka, Bangladesh, Thailand, Indonesia (Java east to Lomblen Island). Not reported from Malaysia or Sumatra.

**HABITAT.**—Primarily inhabits lowland areas. It is common throughout the central dry zone and the Ayeyarwady delta and is often encountered in agricultural areas and paddies as well as open grasslands. Active at night.

**REMARKS.**—Possibly the most common of the dangerously venomous snakes occurring in southern Asia, and responsible for more than half of all reported snakebites. Several color pattern variants have been recognized as distinct subspecies: *Daboia russelii siamensis* from southern China, central and southern Myanmar, and central Thailand; *D. r. formosensis* from eastern China and Taiwan; and the nominate form from India, Pakistan, and Bangladesh. Its unusual distribution, especially its erratic distribution in Indonesia, suggests it has been transported in the course of commercial exchanges, likely during the 18th and 19th centuries. *Daboia russelii* is a prolific breeder and young could easily have been transported among plants and other products that were frequently carried about during the early days of colonial expansion.

Arguments over the correct spelling of the species name, i.e., *russelii* versus *russellii*, abound to this day (most recently, see Adler et al. 2000:83, David and Ineich 1999:313, and McDiarmid, Campbell, and Touré 1999:370). The species was named for Patrick Russell, who spelt his name with a double “ll.” However, there is no indication in the original publication by Shaw and Nodder, or any notice subsequently issued, that their use of the single “l” was a lapsus of any sort. Thus, we follow the original orthography despite the fact that the name of the person being honored is misspelled.

For extended comments on habitat, behavior, reproduction, bite and venoms, see Mallow et al. (2003).

### Subfamily CROTALINAE

#### Genus *Ovophis* Burger, 1981

*Ovophis* Burger in Hoge and Romano-Hoge, 1981:246 (Type species: *Trimeresurus monticola* Günther 1864).

#### *Ovophis monticola* (Günther, 1864)

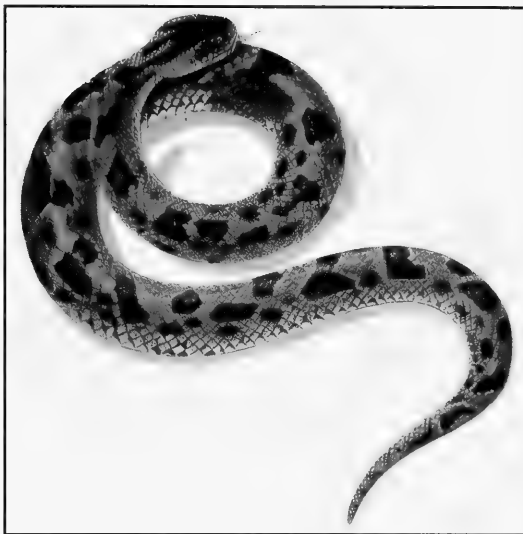
*Trimeresurus monticola* Günther, 1864:388 (Type locality: Nepal and Sikkim; Syntypes: BMNH 1946.1.18.76 and 1946.1.19.91.—Pope, 1935:127, pl. 24D–E and 27A.—Smith, 1943:506, fig. 161.

*Trimeresurus monticola monticola*, Zhao and Adler, 1993:276.

*Ovophis monticola monticola*, Toriba, 1993:81.—Hallermann et al., 2002:152.

*Ovophis monticola*, McDiarmid, Campbell, and Touré, 1999:316.—David and Ineich, 1999:268.

**DIAGNOSTIC CHARACTERS.**— Body stout; snout short, a little more than twice the length of the diameter of the eye; head covered above by small scales rather than large shields, scales usually smooth, feebly imbricate; first upper labial not fused to nasal, completely separated by a suture; body scales, smooth or weakly keeled, in 23–25, occasionally 19 or 21 longitudinal rows at midbody; supraoculars large, 5–9 scales in a line between them; internasals usually not in contact with one another, separated by 2 small suprapostrostral scales; 7–10 upper labials, second usually fused to the scale bordering the facial sensory pit anteriorly, fourth and fifth beneath eye but separated from orbit by 2–4 series of small scales; ventrals and subcaudals (Myanmar, northeastern India and adjacent areas of China and Thailand) 137–176 and 36–62 respectively, subcaudals mixed paired and single, occasionally all unpaired (ventrals and subcaudals for southern China, Vietnam, Laos: 127–144 and 36–54, and Malaysian Peninsula: 133–137 and 22–28 respectively [fide Smith 1943:509]). Total length ♂ 490 mm, ♀ 1100; tail length ♂ 80 mm, ♀ 150 mm.



*Ovophis monticola*. From Fayrer (1874, pl. 15).

**DISTRIBUTION.**— Widely distributed from the eastern Himalayas, Myanmar (Map p. 461), southeastern Xizang (Tibet) and Yunnan, Thailand, southern China and Taiwan, to Vietnam, the Malaysian Peninsula to western Indonesia (Sumatra).

**HABITAT.**— Found in the temperate and subtropical forests of northern Kachin State, from elevations around 1000 m. The altitudinal distribution throughout its range is reported between 700–2400 m (Schleich and Kästle 2002). Individuals have been found in leaf litter and shifting cultivation. Pope (1935) reports that this species is common around villages. Crepuscular (Schleich and Kästle 2002), also secretive and sluggish and most often found tucked away in piles of wood, logs, and rocks, also in rock crevices (David and Vogel 1966).

**REMARKS.**— Zhao and Adler (1993:276) and Toriba (1993:82) recognize several subspecies, the westernmost populations from Nepal, northeastern India, Myanmar, and Yunnan and Szechwan Provinces of China as *Ovophis monticola monticola* (genus *Trimeresurus* in Zhao and Adler); *O. m. convictus* from Cambodia, Vietnam, Thailand, West Malaysia and western Indonesia; *O. m.*



*Ovophis monticola* (JBS 11879) from Kachin, Myanmar. Photo by Hla Tun.

*makazayazaya* from eastern China and Taiwan; and *O. m. zayuensis* from the type locality at Zayü Co, Xizang (Tibet), China. At this time, we take no position on the status of these taxa save that all are clearly members of a “*monticola*” species group.

### Genus *Protobothrops* Hoge and Romano-Hoge, 1983

*Protobothrops* Hoge and Romano-Hoge, 1983:87 (Type species: *Trimeresurus flavoviridis* Hallowell, 1861).

**REMARKS.**— In 1983, Hoge and Romano-Hoge described the new genus *Protobothrops* to accommodate two species previously placed in the genus *Trimeresurus*, *Trimeresurus jerdonii* and *T. mucrosquamatus*. Since that time, few authors have followed their recommendation. More recently, however, Kraus et al. (1996) indicated that preliminary DNA studies support its recognition, though, as pointed out by McDiarmid et al. (1999:329), it was done with some reservation. McDiarmid et al. (*loc. cit.*), thus, chose to take a more conservative approach, pending further studies, and treated *Protobothrops* as a synonym of *Trimeresurus*. In the same year, David and Ineich (1999:274), also citing Kraus et al., as well as additional but unpublished data (received from N. Vidal), decided to recognize *Protobothrops* as a valid genus, though they did note that “the limits of this genus remain provisional.” Of the eight trimeresurid species David and Ineich refer to *Protobothrops*, three occur in Myanmar, *P. jerdonii*, *P. kaulbacki*, and *P. mucrosquamatus*. In this report, we have chosen to follow David and Ineich’s classification scheme.

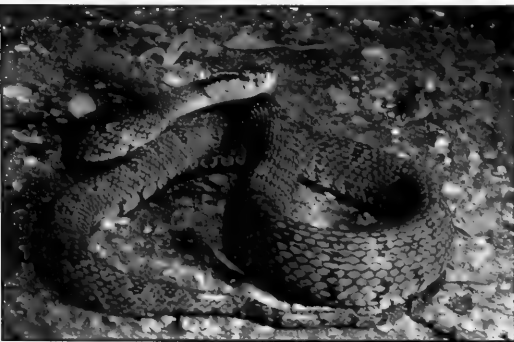
### *Protobothrops jerdonii* (Günther, 1875)

*Trimeresurus jerdonii* Günther, 1875:233, pl. 34 (Type locality: Khasi Hills, India; Syntypes: BMNH 196.1.18.66–68).— Pope, 1935:409, pl. 25.— Smith, 1943:510, fig. 162.— Toriba, 1993:100.— David and Tong, 1997:26, 28.— McDiarmid, Campbell, and Touré, 1999:336.

*Protobothrops mucrosquamatus*, Hoge and Romano-Hoge, 1983:86.— David and Ineich, 1999:275.— David, Captain and Bhatt, 2001:224

**DIAGNOSTIC CHARACTERS.**— Scales in 21 longitudinal rows at midbody (rarely 23); snout length a little more than twice diameter of eye; head above, except for large internasals and supraoculars, covered by small, unequal, smooth scales that are feebly imbricate or juxtaposed; first labial completely separated from nasal by a suture; internasals separated by 1–2 small scales; 6–9 small scales in line between supraoculars; 7–8 upper labials, third and fourth beneath eye, in contact with subocular or separated by at most a single series of small scales; ventrals (see Remarks below): ♂ 164–188, ♀ 167–193; subcaudals: ♂ 50–78, ♀ 44–76. Total length ♂ 835 mm, ♀ 990 mm; tail length ♂ 140 mm, ♀ 160 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 461): Chin State (Chin Hills), Kachin State. ELSEWHERE:



*Protobothrops jerdoni*. Variation in color pattern (CAS 215115 [left] and CAS 215015 [right]). Both individuals from Yunnan Province, China. Photos by Dong Lin.



India (Assam), China (Yunnan, Szechwan, Hupeh).

**HABITAT.**— This species has been recorded in Myanmar and adjacent areas in Yunnan, from elevations of 1442 m to just under 2300 m. In Nepal it has been recorded as high as 2800 m (Schleich and Kästle 2002). Historical records from the Chin Hills and Kachin State as well as recent records from Kachin State place this species in montane (Chin Hills-Rakhine Yoma) and temperate (Northern Triangle) forests. Individuals have been found in shifting cultivation. Orlov et al. (2001) report this species (albeit a different subspecies) as commonly found along rocky streams in trees, shrubs, and under rocks.

**REMARKS.**— Both Pope (1935:409) and Smith (1943:510) took note of the distribution of ventral and subcaudal counts among their samples in relation to their geographic origins. Smith, in particular, notes the following: “Burma, Yunnan (17 examples): V. ♂ 164–173, ♀ 167–189; C. ♂ 50–55 (69), ♀ 44–61. Burma-Tibet border (12 examples): V. ♂ 181–188, ♀ 184–193; C. ♂ 67–78, ♀ 64–76, paired.” Elsewhere in its range, Maslin (1942) chose to recognize the populations from eastern and southeastern China as a distinct subspecies, *Trimeresurus jerdonii xanthomelas* Günther, and Klemmer (1963) referred the populations from Vietnam and Cambodia to *Trimeresurus jerdonii bourreti*. Toriba (1993:100) recognizes both and assigns the remaining populations from Myanmar, northeastern India and the Yunnan and Xizang region of China to the nominate subspecies. The interesting distribution of ventral and subcaudal counts recorded by Smith, apart from the clear indication of sexual dimorphism, suggests the Myanmar-India-southwestern Chinese populations deserve further careful study.

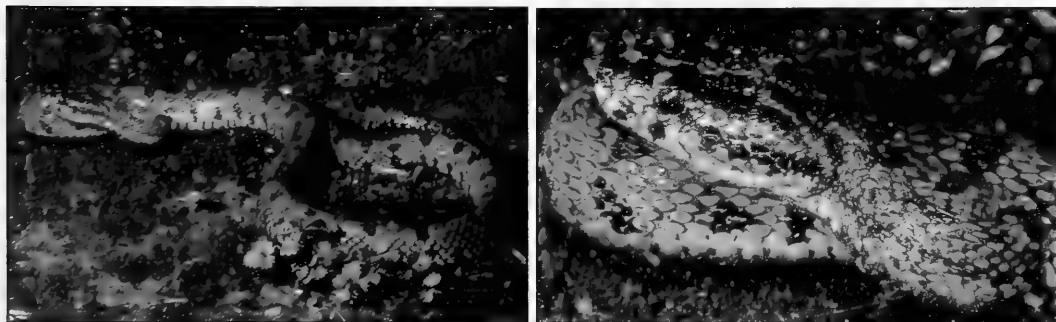
***Protobothrops kaulbacki* (M.A. Smith, 1940)**

*Trimeresurus kaulbacki* Smith, 1940:485, pl. 8, fig. 5 (Type locality: Pangnamdim, north of the Triangle, Upper Burma; Holotype: BMNH 1946.1.19.23–24); 1943:512.— Toriba, 1993:101.— McDiarmid, Campbell, and Touré, 1999:337.

*Protobothrops kaulbacki*, Kraus, Mink, and Brown, 1996:769.— David and Ineich, 1999:276.

**DIAGNOSTIC CHARACTERS.**— Scales in 23–25 longitudinal rows at midbody; body elongate, head long, massive, with narrow snout; canthus rostralis sharp; single large, squarish loreal; first upper labial completely separated from nasal by a suture; second upper labial anteriorly bordering facial pit; 8–10 scales in line between supraoculars; supraoculars usually single, flat, without a vertical projection; dull grayish or olive green with large, blackish rhombohedral dorsal blotches, either distinct or united to one another; smaller spots on sides; symmetrical yellow lines on head; subcaudals paired; ventrals 201–212; subcaudals 66–78, some of the anterior scutes may be single, others paired; hemipenes with spines. Total length ♂ 1340 mm, ♀ 1410 mm; tail length ♂ 225 mm, ♀ 230 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 461): Kachin State (Pangnamdim).



*Protobothrops kaulbacki*. Photos by Hla Tun.

**HABITAT.**— Little is known of the habitat preferences of this rare snake. The lone individual of this species from recent work was found at the type locality (Pangnamdin) at an elevation of 1015 m. This region falls at the transition zone between temperate Northern Triangle forests and eastern alpine shrub and meadow.

***Protobothrops mucrosquamatus* (Cantor, 1839)**

*Trigonocephalus mucrosquamatus* Cantor, 1839:32 (Type locality: Naga Hills, Assam, India; Holotype: Unknown; original description probably based on colored drawing [no. 18] in Bodleian Library, Oxford).

*Trimeresurus mucrosquamatus*, Swinhoe, 1870:411, pl. 31.— Pope, 1935:416, pl. 26.— Smith, 1943:507.— Toriba, 1993:102.— McDiarmid, Campbell, and Touré, 1999:339.

*Protobothrops mucrosquamatus*, Hoge and Romano-Hoge, 1983:86.— David and Ineich, 1999:276.

**DIAGNOSTIC CHARACTERS.**— Scales in 25 longitudinal rows at midbody; scales on upper surface of head, small, each scale keeled posteriorly; internasals 5–10 times size of adjacent scales, separated by 3–4 scales; supraoculars, long, narrow, undivided, 14–16 small interocular scales in line between them; 2 scales on line between upper preocular and nasal; 9–11 upper labials, first upper labial separated from nasal by suture; 2–3 small scales between upper labials and subocular; 2–3 rows of temporal scales above upper labials smooth, above those scales keeled; ventrals 200–218; subcaudals 76–91, all paired; grayish or olive brown above, with dorsal series of large brown, black-edged spots or blotches, and a lateral series of smaller spots; head above brownish, below whitish; belly whitish but heavily powdered with light brown; tail brownish (possibly pink in life [fide Smith 1943:507]), with series of dark dorsal spots; hemipenes spinose. Total length ♂ 1122 mm, ♀ 1160; tail length ♂ 195 mm, ♀ 205 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 461): Kachin State ELSEWHERE: northeastern India and Bangladesh, China, Taiwan and northern Vietnam.

**HABITAT.**— Found in the Northern Triangle temperate and subtropical forests of Kachin State at elevations of 250–1088 m. Individuals have been found near streams either under rocks or in the leaf litter. Pope (1935) reports that the species is common in hilly and mountainous areas. In Vietnam, Orlov et al. (2001) state that the species is common around villages and disturbed habitat. Active at night.

**Genus *Trimeresurus* Lacépède, 1804**

*Trimeresurus* Lacépède, 1804:209 (Type species: *Vipera viridis* Daudin, 1803 [= *Coluber gramineus* Shaw, 1802]).

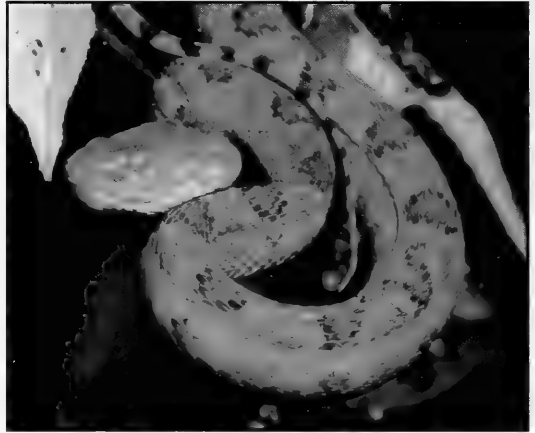
**REMARKS.**— See remarks under Genus *Protobothrops*.

***Trimeresurus albolabris* Gray, 1842**

*Trimeresurus albolabris* Gray, 1842:48 (Type locality: China; Holotype: BMNH 1946.1.19.85).— Smith, 1943:523, fig. 166 [map].— David and Ineich, 1999:280.— McDiarmid, Campbell, and Touré, 1999:329.

*Trimeresurus albolabris albolabris*, Toriba, 1993:95.— David and Tong, 1997:25–26.

**DIAGNOSTIC CHARACTERS.**— Scales in 21 (rarely 19) longitudinal rows at midbody;



*Protobothrops mucrosquamatus*. Photo by Hla Tun.

10–11(12) upper labials, the first partially or completely fused to the nasal; head scales small, subequal, feebly imbricate, smooth or weakly keeled; supraoculars narrow, occasionally enlarged, undivided, 8–12 interocular scales between them; temporal scales smooth; green above, side of head below eyes yellow, white or pale green, much lighter than rest of head; below, green, yellowish or white below, a light ventrolateral stripe present in all males, absent in females; end of tail not mottled brown; ventrals: ♂ 155–166, ♀ 152–176; subcaudals: ♂ 60–72, ♀ 49–66, paired; hemipenes without spines. Total length ♂ 600 mm, ♀ 810; tail length ♂ 120 mm, ♀ 130 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 462): north of 13°N. ELSEWHERE: India (Assam), Thailand, Cambodia, Laos, Vietnam, China, Malaysia, western Indonesia (as far east as Sulawesi).

**HABITAT.**— Often found in heavily degraded forest, or in agricultural areas. Documented to occur in moist mixed deciduous, and subtropical forests (both Northern Triangle and Northern Indochina) as well as temperate forests. This species is commonly encountered in bamboo stands, although individuals have also been found on trees, in bushes, on the ground in open fields, and crossing roads. Elevations range from 60–751 m in Myanmar, although it is recorded as high as 3050 m in Nepal (Schleich and Kästle 2002). Active at night. David and Vogel (1996) note that it prefers lowland habitats, both forested and open, and when in bushes or trees, usually within 2 or 3 m of the ground.

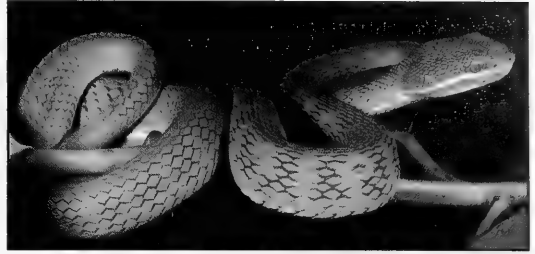
**REMARKS.**— Two subspecies have been described, *T. a. insularis* Kramer (1977) from eastern Indonesia (Soe and Timor) and *T. a. septentrionalis* Kramer (1977) from Nepal and northwestern India (Simla).

### *Trimeresurus erythrurus* (Cantor, 1839)

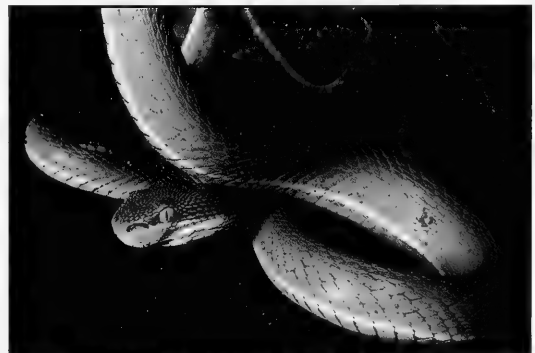
*Trigonodactylus erythrurus* Cantor, 1839:31 (Type locality: Ganges Delta; Holotype: BMNH 1946.1.19.99).

*Trimeresurus erythrurus*, Smith, 1943:386, fig. 165.— Toriba, 1993:97.— David and Ineich, 1999:283.— McDiarmid, Campbell, and Touré, 1999:331.

**DIAGNOSTIC CHARACTERS.**— Scales in 23–25 longitudinal rows at midbody; first upper labial partially or completely fused to nasal; 9–13 upper labials, 1–2 rows of scales separate upper labials from subocular; 11–14 scales in a line between supraoculars; supraoculars rarely divided; temporal scales small, strongly keeled; ventrals: males 153–174, females: 151–180; subcaudals: ♂ 62–79, ♀ 49–61, usually paired, occasionally unpaired shields present among paired series; head uniform green, dorsum bright green, light ventrolateral stripe present in males, present or absent in females (Maslin [1942:23] says that the ventrolateral stripe is absent, but Smith [1943:524] states that it is present in males and variable in females), tail spotted with brown; hemipenes without spines. Total length ♂ 575 mm, ♀ 1045; tail length ♂ 120 mm, ♀ 165 mm.



*Trimeresurus albolabris*. Photo by Hla Tun.



*Trimeresurus erythrurus*. Photo by Dong Lin.

**DISTRIBUTION.**—MYANMAR (Map p. 462): Sagaing State, Kachin State, Rakhine State, Yangon Division. *T. erythrurus* is found west of Long. 98°. ELSEWHERE: India (northeastern India from Bengal to Assam, east of Long. 88°) east through Bangladesh.

**HABITAT.**—Individuals of this species have been found in rainforests (Myanmar coastal, Mizoram-Manipur-Kachin) and moist deciduous forest. Elevations are recorded under 200 m. Individuals have been met with in trees and on the ground near streams. Active at night.

*Trimeresurus medoensis* Zhao, 1977

*Trimeresurus medoensis* Zhao in Zhao and Jiang, 1977:66, pl. 2, fig. 9, 1–5 (Type locality: near Ani Bridge, Motuo, Xizang, at 1200 m; Holotype: CIB 73-II-5208).—Toriba, 1993:103.—McDiarmid, Campbell, and Touré, 1999:339.—David and Ineich, 1999:287.—David et al., 2001:218.—David, Captain and Bhatt, 2002:210–226, figs. 1–7.

**DIAGNOSTIC CHARACTERS.**—Scales in 17 longitudinal rows at midbody, dorsal rows 7–11 slightly keeled; 8 upper labials, first upper labials separated from nasals by a distinct suture; green or bluish green above, yellowish white below, the two separated by a bright bicolored red (below) and white (above) ventrolateral stripe (in both males and females), which occupies the whole of the outermost scale row and a portion of the second row; ventrals less than 150; hemipenes short, thick, spinose. Total length ♂ 671 mm, ♀ 650; tail length ♂ 125 mm, ♀ 115 mm.



*Trimeresurus medoensis*. Photo courtesy Ashok Captain.

**DISTRIBUTION.**—MYANMAR (Map p. 462): Kachin State (Naung Mon, Rainbow Village, Myitkina; Alangdunhku). ELSEWHERE: China (Xizang Autonomous Region); India (Arunachal Pradesh) (after David et al. 2001:218; David et al. 2002:210 ff.).

**HABITAT.**—The only records of this species in Myanmar are from Kachin State. Three specimens from Nam Ti Valley are referenced in the original description (Zhao 1977), and their identifications are confirmed by David et al. (2001). A specimen from the Myitkina area is also referable to this species (David et al. 2001). David et al. (2001) and Das (2002) report this snake as frequenting bamboo stands in otherwise evergreen forest. The lone specimen from recent collections made by members of the Myanmar survey team was found near a trail in low elevation evergreen forest that was interspersed with bamboo stands where the forest had been altered. Active at night (Das 2002).

*Trimeresurus popeiorum* M.A. Smith, 1937

*Trimeresurus popeiorum* Smith, 1937:730 (Type locality: Sikkim, India; Holotype: BMNH 72.4.17.137.—David and Ineich, 1999:288.—David, Captain, and Bhatt, 2002:218, 223.

*Trimeresurus popeiorum*. Smith, 1943:518.—Toriba, 1993:103.—McDiarmid, Campbell, and Touré, 1999:340.

*Trimeresurus popeiorum popeiorum*, David et al., 1997:27.

**DIAGNOSTIC CHARACTERS.**—Scales in 21 (rarely 23) longitudinal rows at midbody; 9–11 upper labials, first upper labials separated from nasals by a distinct suture; a single supraocular;

above green, below pale green to whitish, the two separated by a bright bicolored orange or brown (below) and white (above) (males) or white (females) ventrolateral stripe, which occupies the whole of the outermost scale row and a portion of the second row; ventrals 155–169; subcaudals 52–76, in males the base of the tail enlarged to the level of subcaudals 20–25; hemipenes long and slender, smooth, without spines. Total length 770 mm, tail length 170 mm.



*Trimeresurus popeiorum*. Photo by John Tashjian.

**DISTRIBUTION.**—MYANMAR (Map p. 462):

Bago Division, Mon State, Tanintharyi

Division, and (?) Chin State. ELSEWHERE: Laos; Vietnam; Cambodia; Malaysia; Singapore; Indonesia (Kalimantan, Sumatra), (?) Thailand (see David et al. [2001:218]).

**HABITAT.**—In Peninsular Malaysia and Singapore, this nocturnal species is reported from montane forests (Lim and Lee 1986) with elevations from 900–1500 m (Cox et al. 1998). Elsewhere, it has been found in hilly areas with wet forest (David and Vogel 1996). In Myanmar, it has been found in low elevation (less than 500 m) montane and coastal rainforest. Individuals have been collected on tree limbs overhanging streams and in bushes. Active at night.

**REMARKS.**—Most often confused with *T. stejnegeri* (q.v.), the two have quite distinct hemipenes, which does not make identification of individuals in the field or in the laboratory any easier without recourse to (a) male individuals and (b) an examination of the hemipenes. However, the two species are not known to have overlapping distributions, at least based on available materials. Also, closely allied to *T. popeiorum* is *T. yunnanensis* (q.v.); ordinarily, the two are more easily be told apart by the number of midbody scale rows, 21 in *T. popeiorum*, 19 in *T. yunnanensis*.

The species name “*popeiorum*” has been variously spelt “*popeiorum*” and “*popeorum*.” In the original description, it was given as “*popeiorum*,” but in 1943, in the footnote on p. 518, Smith states “*Popeiorum* as originally spelt is a clerical error.” Although a clerical error, yet the use of “*popeorum*” contravenes Article 32(c)(ii), which states that an original spelling is an ‘incorrect original spelling’ if “there is in the original publication itself, without recourse to any external source of information, clear evidence of an inadvertent error . . . (. . . and use of an inappropriate connecting vowel are not to be considered inadvertent errors).” Because there is no such evidence in the original publication, *Trimeresurus popeiorum* must stand as the appropriate spelling for the nominal species meant to honor Clifford H. Pope.

### *Trimeresurus purpureomaculatus* Gray, 1830

*Trigonocephalus purpureomaculatus* Gray in Gray and Hardwicke, 1830:pl. 81 (Type locality: Singapore;

Holotype: BMNH 1946.1.19.54 and Hardwicke’s sketch no. 158).

*Trimeresurus purpureomaculatus purpureomaculatus*, M.A. Smith, 1943:520.—Toriba, 1993:104.

*Trimeresurus purpureomaculatus*, David and Ineich, 1999:280.—McDiarmid, Campbell, and Touré, 1999:42.

**DIAGNOSTIC CHARACTERS.**—Scales in 25–27 longitudinal rows at midbody; 11–13 upper labials, the first partially or completely united with the nasal; supraocular very narrow, sometimes broken into small scales, 12–15 scales between them; head scales small, subequal, tuberculate or granular; temporal scales keeled; body color highly variable, above olive, grayish, to dark purplish brown, below whitish, greenish or brown, uniform or spotted with brown; a light line on scale row

one bordering ventrals present or absent; head olive, heavily suffused with brown; ventrals: ♂ 160–179, ♀ 168–183; subcaudals: ♂ 74–76, ♀ 56–63, paired; hemipenes without spines. Total length ♂ 665 mm, ♀ 900; tail length ♂ 125 mm, ♀ 140 mm.

**DISTRIBUTION.**—MYANMAR (Map p. 462): Ayeyarwady Division, Mon and Karen States south of Lat. 17°N, Tanintharyi Division. ELSEWHERE: Malaysia, Singapore, western Indonesia (Sumatra).

**HABITAT.**—This species has been found in abundance in the remaining mangrove forests of the Ayeyarwady Delta. Lim and Lee (1986) similarly report this species from mangrove forests on offshore islands and mainland peninsular Malaysia and Singapore. David and Vogel (1996) report that in Sumatra it is found in mangrove and coastal swamp habitats, in marshes, and along canals and river banks. Individuals have been found in trees and shrubs. Crepuscular.

**REMARKS.**—A population of Asian pit vipers that is closely allied to *T. purpureomaculatus* occurs on the Andaman and Nicobar Islands. In 1868, Theobald described it as a new species, *T. andersoni*. Since then it has been variously treated as a synonym of *T. purpureomaculatus* or as a subspecies of the latter. In view of its complete isolation from mainland *T. purpureomaculatus* and its distinguishing features (see Smith 1943:520–521), we take the position that it is best treated as a distinct species. We do recognize that it was derived from a population of *T. purpureomaculatus* that inhabits a neighboring area, but which of the neighboring areas we do not know.



*Trimeresurus purpureomaculatus*. Photo by Dong Lin.

### *Trimeresurus stejnegeri* K.P. Schmidt, 1925

*Trimeresurus stejnegeri* K.P. Schmidt, 1925:4 (Type locality: Shaowu, Fukien, China; Holotype: AMNH 21054).—Pope, 1935:409, pl. 25.—Smith, 1943:517.—McDiarmid, Campbell, and Touré, 1999:344.—David and Ineich, 1999:290.—David, Vidal and Pauwels, 2001:205, 218, 221.—David, Captain and Bhatt, 2002:218, 221, 223.—Hallermann et al., 2002:152.

*Trimeresurus stejnegeri stejnegeri*. Maslin, 1942:22.—Toriba, 1993:105.

**DIAGNOSTIC CHARACTERS.**—Scales in 21 longitudinal rows at midbody; 9–11 upper labials, first upper labials separated from nasals by a distinct suture; a single narrow supraocular, sometimes divided by transverse suture; 11–16 scales in a line between supraoculars; above bright to dark green, below pale green to whitish, the two separated by a bright bicolored orange or brown (below) and white (above) (males) or bicolored or white only (females) ventrolateral stripe, which occupies the whole of the outermost scale row and a portion of the second row; ventrals 150–174, subcaudals 54–77 (but see David et al. [2002:218 and 2001:215] for geographic distribution of these data), all paired; hemipenes short, spinose beyond bifurcation. Total length 750 mm, tail length 145 mm.

**DISTRIBUTION.**—All records of this species from MYANMAR have been referred to *Trimeresurus yunnanensis* (see below). ELSEWHERE: China (central and southeastern), Taiwan, Vietnam. For possible northeast Thailand occurrence, see David et al. (2001:218–219).

**HABITAT.**—Pope (1935) reports that this nocturnal species is very common around fast-flowing streams. Elevations are recorded from 500–900 m (*ibid.*).

**REMARKS.**—See remarks under *T. yunnanensis* (below).

*Trimeresurus yunnanensis* K.P. Schmidt, 1925

*Trimeresurus yunnanensis* K.P. Schmidt, 1925:4 (Type locality: Tengyueh [=Tengchiong Co.], Yunnan, China; Holotype: AMNH 21058).— David and Tong, 1997:26–27.— David and Ineich, 1999:294.— David, Vidal and Pauwels, 2001:218.— David, Captain and Bhatt, 2002:218, 221, 223.

*Trimeresurus stejnegeri*, Smith, 1943:517 (part).

*Trimeresurus stejnegeri yunnanensis*, Maslin, 1942:22.— Toriba, 1993:106.

**DIAGNOSTIC CHARACTERS.**— Scales in 19 (rarely 21) longitudinal rows at midbody and 19(–21) on neck; 9–10 (rarely 11) upper labials, first upper labials separated from nasals by a distinct suture; a single narrow supraocular, sometimes divided by transverse suture; 11–16 scales in a line between supraoculars; above bright to dark green, below pale green to whitish, the two separated by a bicolor orange or brown (below) and white (above) (males) or white only or absent (females) ventrolateral stripe, which occupies the whole of the outermost scale row and a portion of the second row; ventrals 155–165 (–170); subcaudals (58–) 61–68, all paired; hemipenes short, spinose beyond bifurcation. Total length 750 mm, tail length 145 mm.

**DISTRIBUTION.**— MYANMAR (Map p. 462):Chin State (Haka); Kachin State. ELSEWHERE: China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, Jilin, Sichuan, Yunnan, Zhejiang); Taiwan; Vietnam (Lao Cai, Vinh Phú, and possibly Bac Thai, Da Nang, Gia Lai, and Hoa Binh); Laos (after David et al. 2001:218).

**HABITAT.**— Recorded at 1206 m in the mountainous regions of Yunnan in Nujiang Langcang Gorge alpine conifer and mixed forest. Das (2002) (as *T. stejnegeri*) reports this species at elevations up to 2845 m. Historical records for Myanmar place this species in subtropical forests (northern triangle) and Chin Hills-Rakhine montane forest. Individuals have been recorded in bushes and trees and on the ground in grass (Pope 1935), also from grassy slopes with shrubs as well as mixed forest (Schleich and Kästle 2002).

**REMARKS.**— This species has been variously treated as a subspecies of *T. stejnegeri* and as a distinct species allied to *T. stejnegeri*. David et al. (2001) have referred all specimens previously identified as *T. stejnegeri* coming from Myanmar to *T. yunnanensis*, and they have restricted *T. stejnegeri* to China, Taiwan, Vietnam and Laos. A specimen identified as *T. stejnegeri* in the Natural History Museum London, reportedly from Chin State, is considered by David et al. to be “an atypical specimen of *T. yunnanensis*” (David et al. 2001:219). If David et al. are correct, then *Trimeresurus stejnegeri* should probably be removed from the faunal list for Myanmar, although the “*stejnegeri*” clade is still represented in the country by *T. yunnanensis* and *T. medoensis* (q.v.). Nonetheless, as we pointed out earlier (p. 409), there is a good possibility that *T. stejnegeri* (*sensu stricto*) will turn up in eastern Shan and Kachin States,<sup>4</sup> and for this reason, it is still listed here (see above). On the other hand, we also concur with David et al. (2001:219) who argue, with justification, that considerable work remains to be done and material examined from throughout the southern ranges (from northeastern India to Vietnam) of the several recognized nominal species to understand species boundaries within the “*stejnegeri*” clade.

## LITERATURE CITED

NOTE: Not included in this section are full bibliographic citations for most pre 20th century literature even though reference is made to them in the synonymies (e.g., Schneider, 1799, 1801; Cantor, 1839; Gray, 1834, 1842, 1849; Laurenti, 1768; Linnaeus, 1758, Schmidt, 1925, and others). Complete citations to these will be found in the bibliography in GOLAY ET AL. 1993 (q.v.).

<sup>4</sup> N.B. Hallermann et al. (2002) identified one of Leonardo Fea's specimens collected at “Mti. Carin [=Karen], 900–1000 m a.s.l. (ZMH R06267-8)” (Kayah State) as *T. stejnegeri*. Kayah State is immediately south of Shan State.

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APPENDIX A

SNAKEBITE PROCEDURES IN MYANMAR

Prepared by Joseph B. Slowinski, Ph.D.

**NOTICE:** A word of caution. The following guidelines were formulated from recommendations made in the WHO/SEARO Guidelines for the Clinical Management of Snakebites in the Southeast Asian Region (1999), written and edited by Dr. David Warrell, and from specific comments made by Dr. David Warrell. However, recommendations and medical procedures undergo constant review and revision; thus, the reader is cautioned to seek the latest information and guidance from appropriate medical specialists before adopting any of the recommendations cited below.

In case of a bite from any species in the family Elapidae or Viperidae or a bad bite from a *Rhabdophis subminiatus*, the bitten person must be transported to a hospital as soon as possible. Do not allow traditional treatments; they will only delay transport to the hospital and can even cause additional damage. Although a bite from a venomous snake should be considered a medical emergency, the victim should be reassured and calmed as much as possible. During the transport process to the hospital, the victim should move as little as possible—any muscle contractions will increase systemic absorption of the venom. With treatment, the chances of dying from a venomous snakebite are small.

The best hospital has the following:

- 1) antivenom;
- 2) epinephrine to treat anaphylaxis;
- 3) a system for assisted breathing in the case of neurotoxicity from an elapid bite;
- 4) treatment for acute kidney failure.

**Russell's viper (*Daboia russelii*).** Do not apply first aid, do not allow the patient to walk, proceed immediately to a hospital and request antivenom for *Daboia russelii* from the Myanmar Pharmaceutical Industry. Severe systemic symptoms such as incoagulable blood, hemorrhage, shock, and kidney failure can develop rapidly from bites by this species. At the hospital, blood coagulability should be tested, which can be done by the 20-minute whole blood clotting test (see below). The hospital should be prepared to treat the kidney failure that often results from bad bites by this species.

**Monocled cobra (*Naja kaouthia*).** Do not apply first aid, do not allow the patient to walk, proceed immediately to a hospital and request antivenom for *Naja kaouthia* from the Myanmar Pharmaceutical Industry. If breathing becomes difficult because of severe neurotoxicity—whether or not antivenom has been administered—the patient should be placed on assisted breathing. Neuromuscular transmission can often be dramatically improved with an anticholinesterase drug such as neostigmine or edrophonium. Atropine should be given as well.

**Spitting cobra (*Naja mandalayensis*).** Do not apply first aid, do not allow the patient to walk, proceed immediately to a hospital. Do not accept antivenom. If breathing becomes difficult because of severe neurotoxicity (this species may or may not cause neurotoxicity; there is no published information on the clinical effects of its venom), the patient should be placed on assisted breathing. Neuromuscular transmission can often be dramatically improved with an anticholinesterase drug such as neostigmine or edrophonium. Atropine should be given as well. There is anecdotal evidence that the venom of this species can cause severe local effects, including necrosis.

In the case of spitting cobra venom spat in the eyes, the eyes should be immediately flushed with generous amounts of water. Do not accept the traditional treatment of tamarind leaf juice in the eyes. Apply topical antibiotic unless corneal abrasions can be excluded by fluorescein staining or slit lamp examination.

**King cobra (*Ophiophagus hannah*).** Apply a compression bandage to the bitten limb, do not allow the patient to walk, proceed immediately to a hospital. Do not accept antivenom, unless they have antivenom specifically made for king cobras in India or Thailand. If breathing becomes difficult because of severe neurotoxicity—whether or not antivenom has been administered—the patient should be placed on assisted breathing. Neuromuscular transmission can often be dramatically improved with an anticholinesterase drug such as neostigmine or edrophonium. Atropine should be given as well.

**Elapid seasnake (*Hydrophis*, *Lapemis*, other genera).** Apply a compression bandage to the bitten limb, do not allow the patient to walk, proceed immediately to a hospital. Do not accept antivenom. If breathing becomes difficult because of severe neurotoxicity, the patient should be placed on assisted breathing. Neuromuscular transmission can often be dramatically improved with an anticholinesterase drug such as neostigmine or edrophonium. Atropine should be given as well. Note: local symptoms from bites by this group may be minimal and should not be taken as a sign of no envenomation.

**Krait (*Bungarus*).** Apply a compression bandage to the bitten limb, do not allow the patient to walk, proceed immediately to a hospital. Do not accept antivenom. If breathing becomes difficult because of severe neurotoxicity, the patient should be placed on assisted breathing. Neuromuscular transmission can often be dramatically improved with an anticholinesterase drug such as neostigmine or edrophonium. Atropine should be given as well. Note: local symptoms from bites by this genus may be minimal and should not be taken as a sign of no envenomation.

**Coral snake (elapid genera *Maticora* (= *Calliophis*), *Calliophis*, *Sinomicrurus*).** Do not

apply first aid, do not allow the patient to walk, proceed immediately to a hospital. Do not accept antivenom. If breathing becomes difficult because of severe neurotoxicity, the patient should be placed on assisted breathing. Neuromuscular transmission can often be dramatically improved with an anticholinesterase drug such as neostigmine or edrophonium. Atropine should be given as well.

**Vipers (other than *Daboia*) (*Ovophis*, *Protobothrops*, *Trimeresurus*).** Any viperid other than the Russell's viper (e.g., *Trimeresurus*). Do not administer first aid; proceed immediately to a hospital, do not accept antivenom.

**Red-necked keelback (*Rhabdophis subminiatus*).** If the bite was bad (i.e., the snake chewed the skin for more than several seconds), do not administer first aid, proceed immediately to a hospital, do not accept antivenom. The blood should be tested for incoagulability. Note: the bad symptoms from this species may take more than a day to develop.

### Antivenom Rules

- 1) Antivenom should only be administered if there are signs of local or systemic envenomation.
- 2) Before antivenom is injected, epinephrine must be available to counter anaphylaxis. If the need arises to inject epinephrine, an antihistamine should also be applied to neutralize histamine release during the allergic reaction.
- 3) Under no conditions should you allow antivenom from a species other than the one that bit the victim to be administered.
- 4) Under ordinary circumstances, do not accept antivenom made in other countries, except possibly in case of a bad king cobra bite.
- 5) The doctor should monitor the patient for adverse reactions for at least one hour after antivenom is administered.

### Definitions and Explanations

**20-minute whole blood clotting test.** A very simple test to perform. Place a few ml of blood into a glass container; leave undisturbed for 20 minutes; tip the vessel once. If the blood is still liquid and runs out, the patient has incoagulable blood, a sign of systemic poisoning.

**Anaphylaxis.** A potentially life-threatening allergic reaction to foreign molecules characterized by a dramatic drop in blood pressure. With snakebite, anaphylaxis can develop in two ways: in response to the venom or in response to the antivenom. When antivenom is administered it is important for the hospital to have epinephrine nearby to counteract a possible anaphylactic reaction.

**Neurotoxicity.** The venoms of cobras, kraits, and sea snakes are dominated by neurotoxins, compounds that adversely affect the nervous system. Symptoms of neurotoxic poisoning include loss of muscle control, which often is manifested by drooping eyelids and loss of muscle tone in other facial features. The major effect — and the deadly one — is the paralysis of the diaphragm resulting in the inability to breathe. This is the reason for the necessity of assisted breathing mechanisms.

**Antivenom.** Antivenom is generally manufactured in horses. A large dose of antivenom causes the body to react to the serum and so severely that the body's immunological reaction is so strong as to cause shock and possibly death from the antivenom. Epinephrine counteracts the immunological reaction and reduces shock. Antivenom is dangerous for the reason described above and is highly species specific. Taking an antivenom for another snake species has no medical value

because it will not counteract the venom of a different species, and it threatens the snakebite victim because of the potential immunological reaction to the serum. The antivenoms produced in Myanmar use venom from Myanmar snakes. Because the venoms from the same species in different geographic areas may differ, it is essential that you use Myanmar antivenoms to ensure that the antivenom works to counter the venom injected by a Myanmar species. The Myanmar Pharmaceutical Industry manufactures antivenom against bites from Russell’s vipers and monocled cobras.

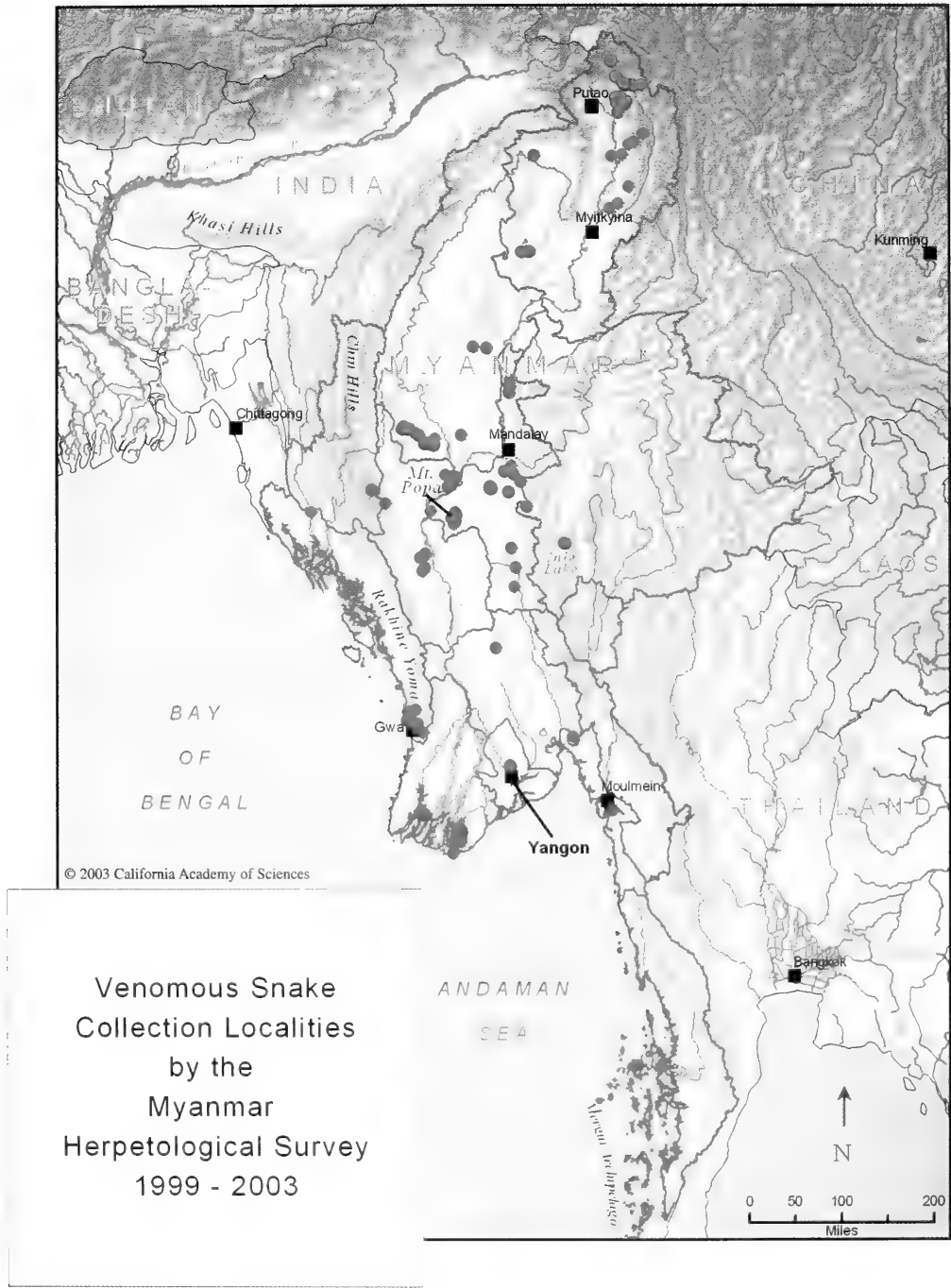
**Compression bandage.** The above recommendations for and against the use of compression bandages are based on a consideration of a venom’s potential to cause local tissue damage versus its potential to cause life-threatening systemic symptoms. A compression bandage should be applied as tightly as for a sprained ankle. It should not be applied so tightly that it eliminates the bitten limb’s pulse. A compression bandage applied to a bitten limb will retard the venom’s absorption by the body, but traps venom in that compartment running the risk of amplified local tissue damage. The venom of kraits is known to be highly toxic, yet does not cause serious local tissue damage. Hence, there is little risk of tissue damage by applying the bandage, only the benefit of retarding venom spread until a hospital is reached. On the other hand, the venom of snakes of the genus *Trimeresurus* have the potential to cause severe local tissue damage, which will be made much worse by the application of a compression bandage.

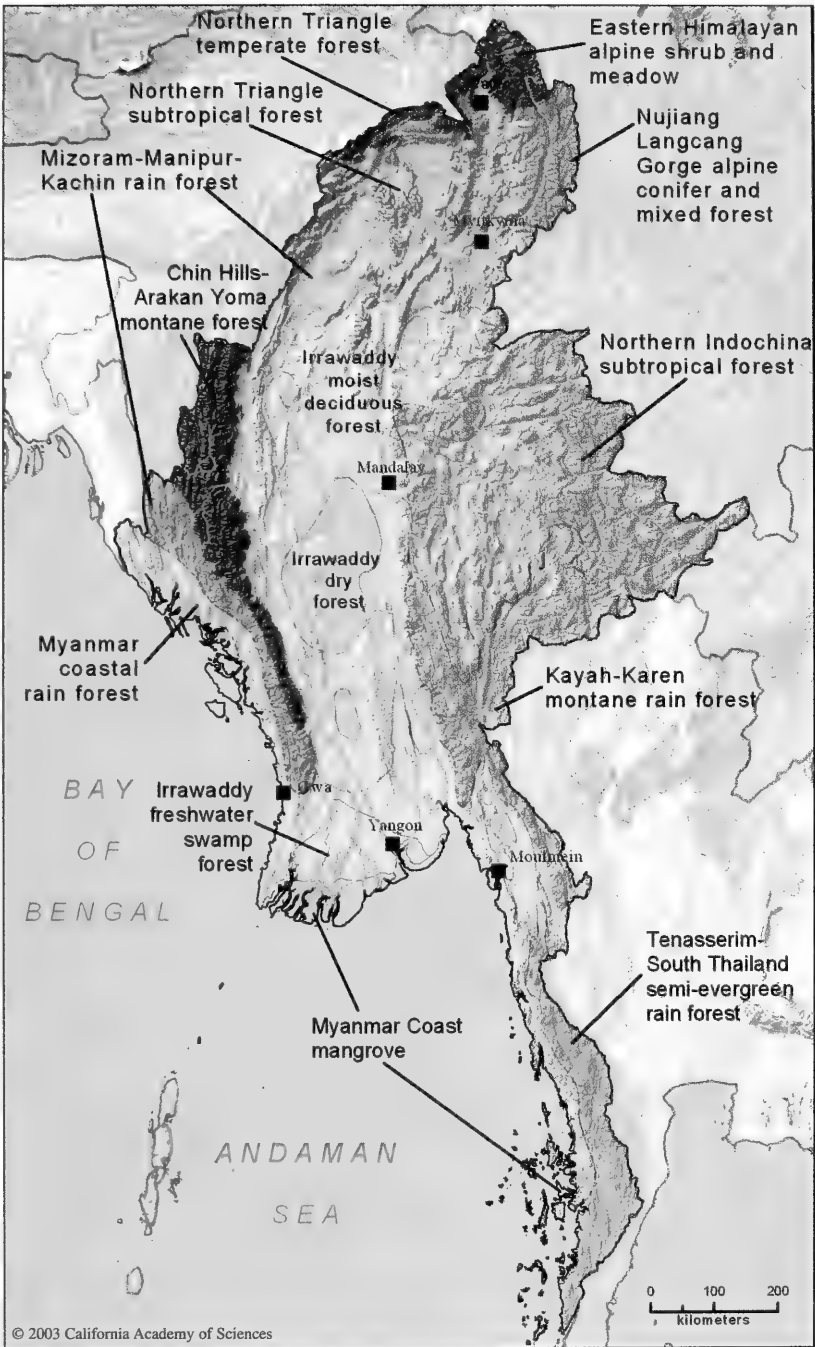
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**MAPS**  
**Locations of dangerously venomous**  
**snake materials collected by**  
**Myanmar Herpetological Survey**  
**teams 1999–2003**  
**with additional localities taken**  
**from literature records**

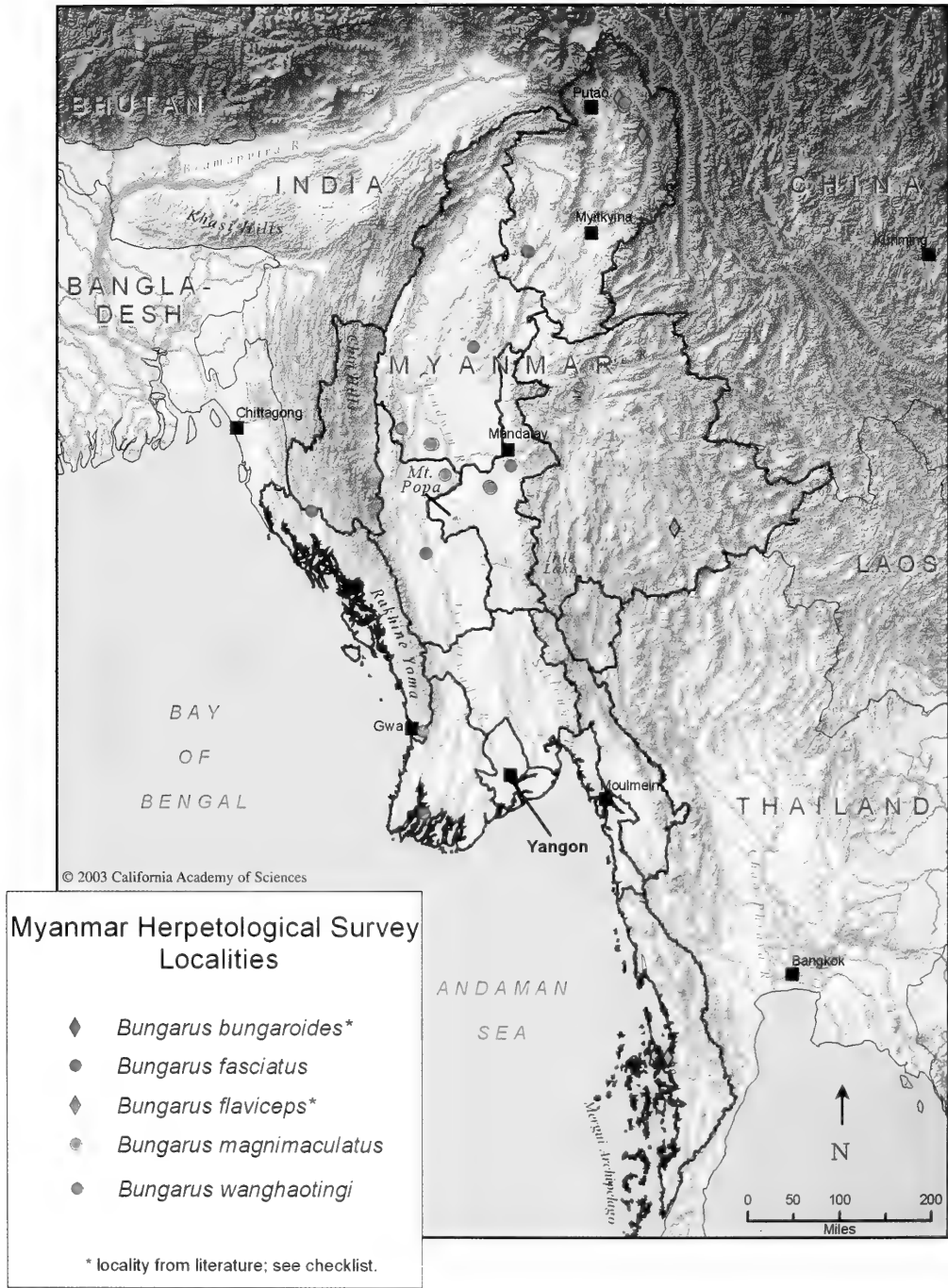
**Note:** Maps are digitally rendered using ArcGIS® (ESRI) and source material from U.S. Geological Survey (USGS), National Imagery and Mapping Agency (NIMA), and Australian Centre of the Asian Spatial Information and Analysis Network (ACASIAN).  
Inspiration for the Myanmar Ecosystem map came from reading Olson, David M., et al. 2001. Terrestrial ecoregions of the World: A new map of life on Earth. *BioScience* 51(11).

All maps were prepared by Michelle S. Koo, Biogeographic Information Systems Manager, Department of Herpetology, California Academy of Sciences

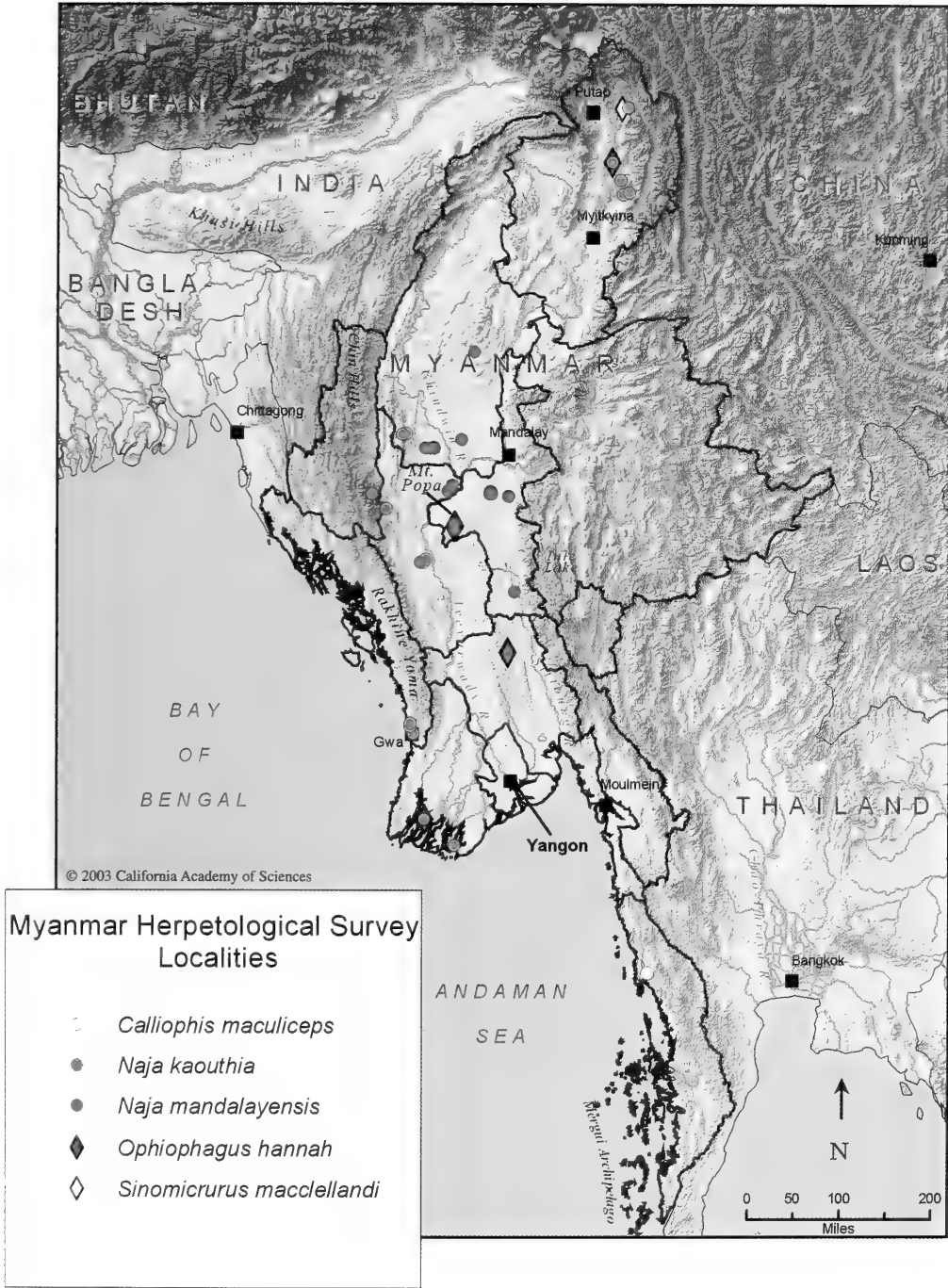


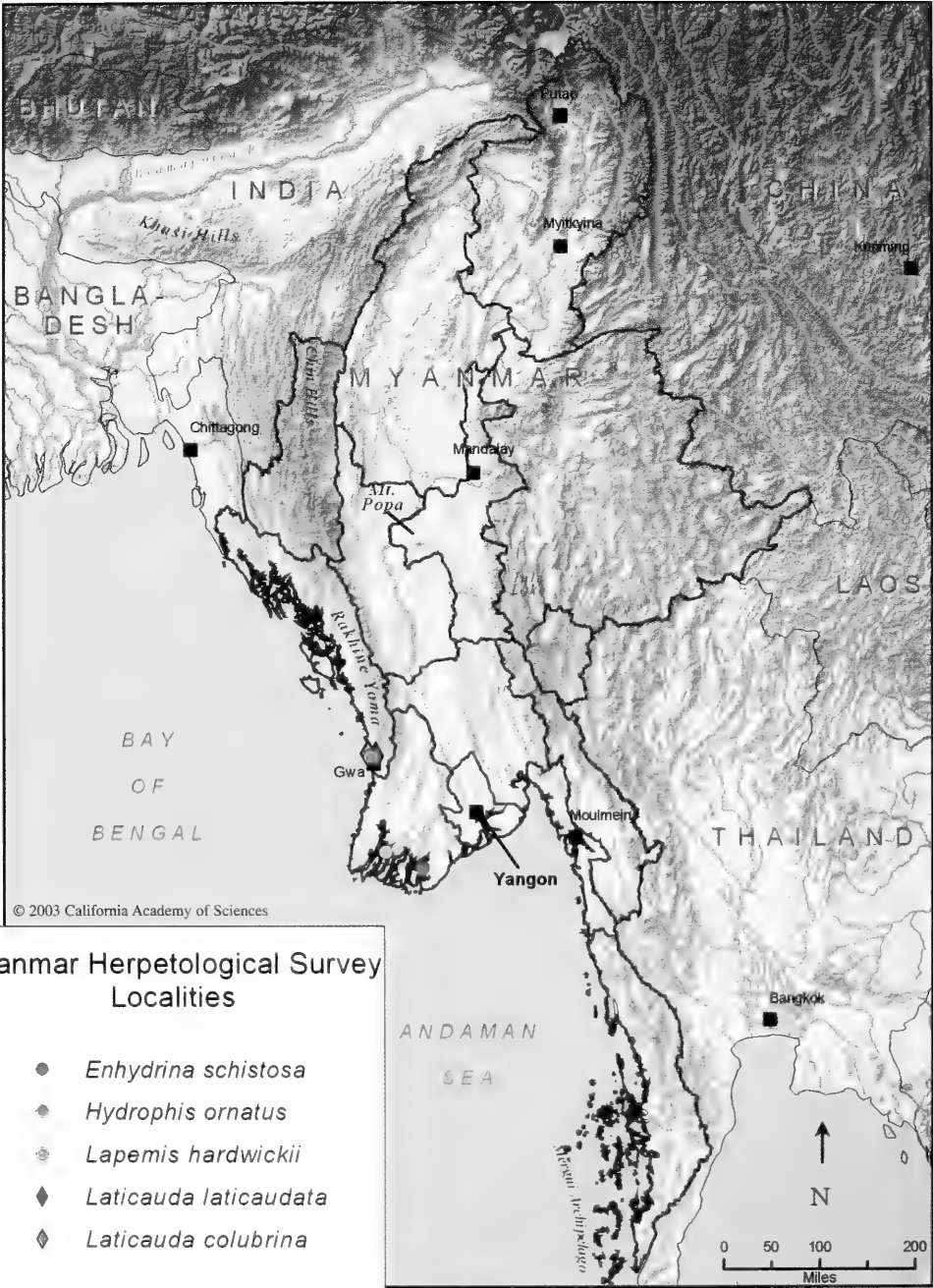


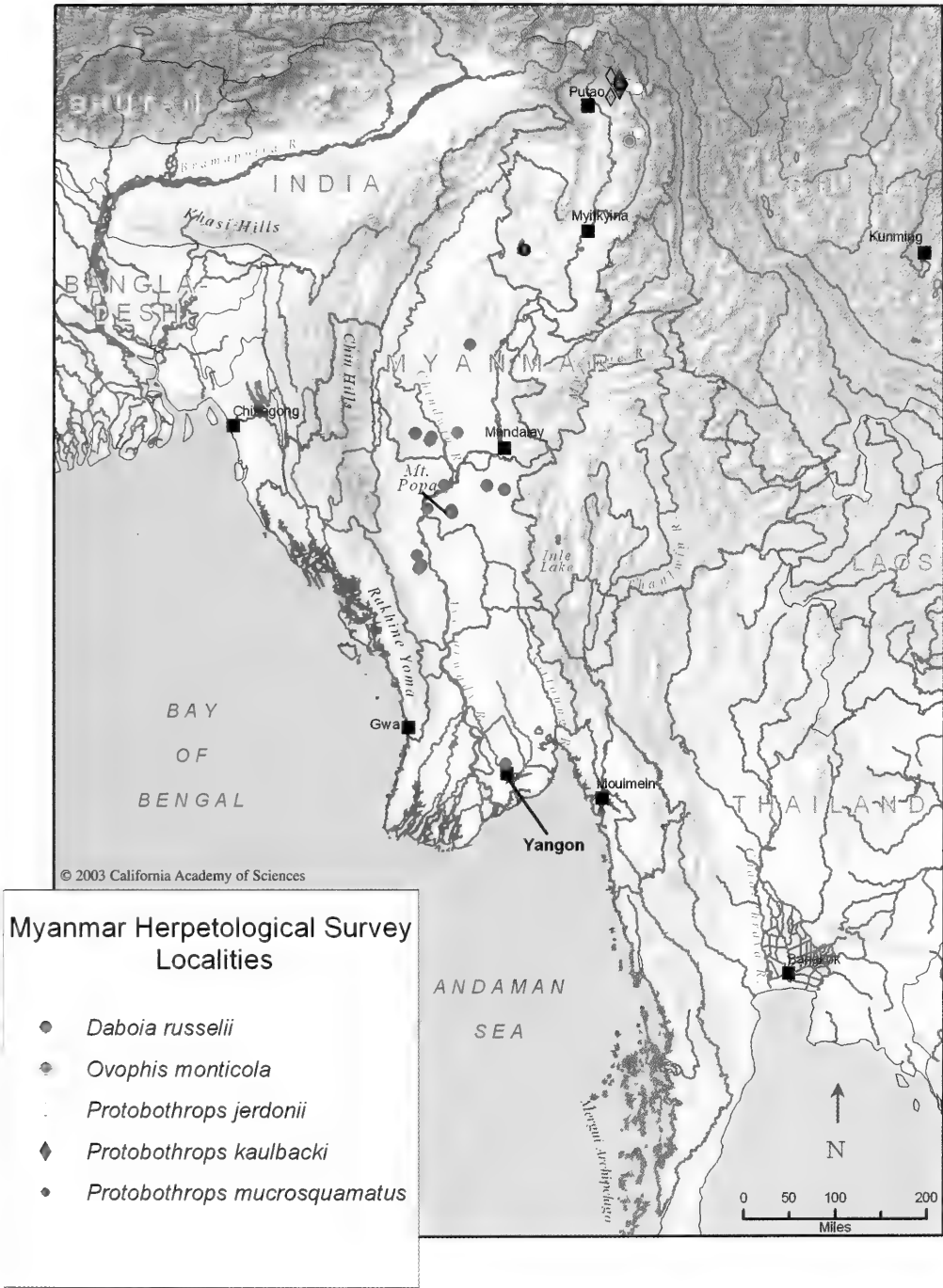
Ecoregions of Myanmar

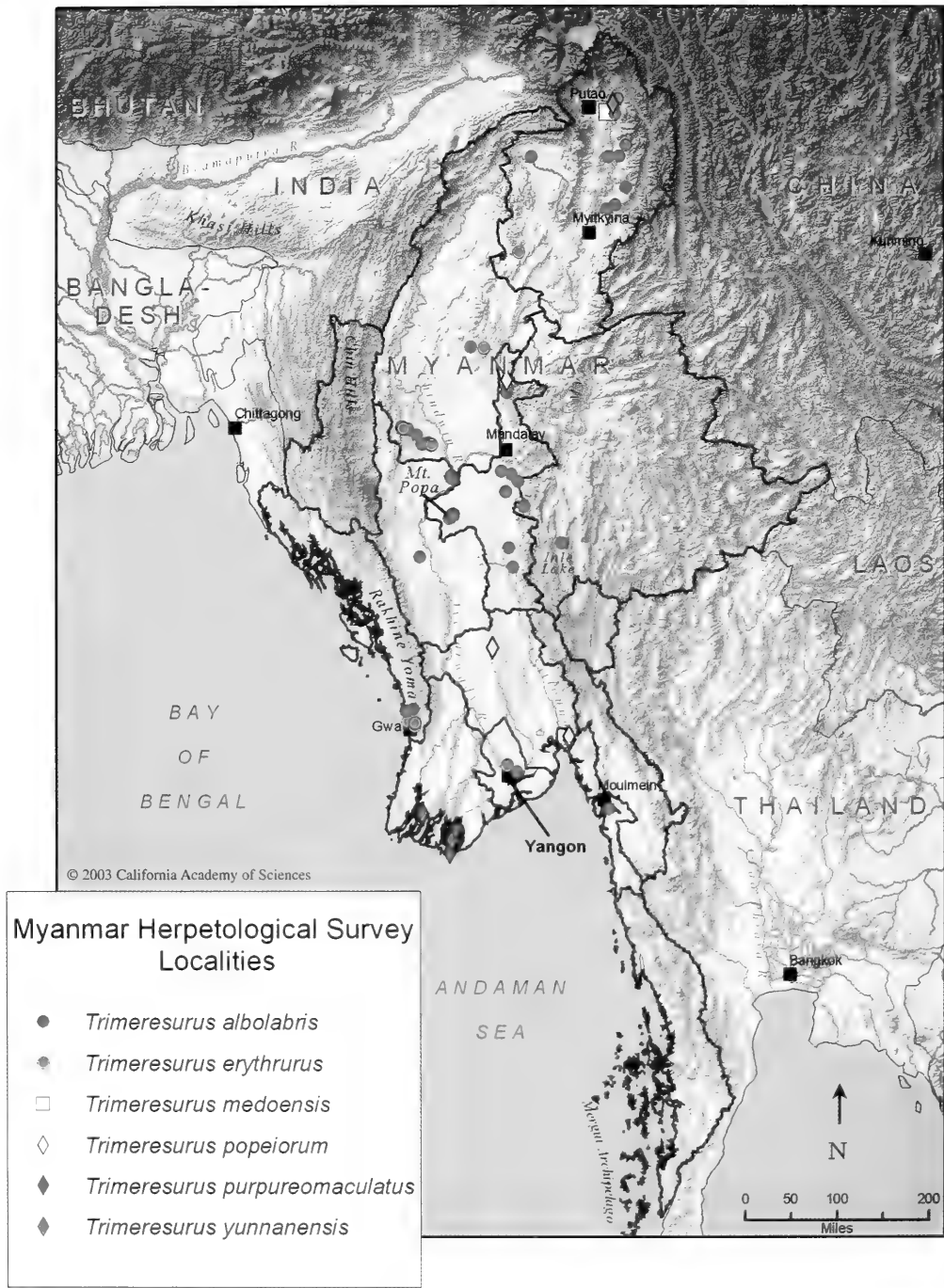












## Descriptions of Seven New *Cyrtodactylus* (Squamata: Gekkonidae) with a Key to the Species of Myanmar (Burma)

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Seven new species of the gekkonid lizard genus *Cyrtodactylus* are described on the basis of material collected by the Myanmar Herpetological Survey. These include four small to moderately sized species with relatively short digits and three larger species with long, slender digits. Among the smaller forms two are allied to *C. khasiensis*; one from the Ayeyarwady delta and adjacent lowlands, the other from higher elevations in the Chin Hills. The remaining small species, from Alaungdaw Kathapa National Park (Sagaing Division) and Rakhine Yoma Elephant Range (Rakhine State) are probably most closely allied to *C. consobrinoides*. The large-bodied forms include the apparent sister species of *C. slowinskii*, from far northwestern Myanmar, and two other, distinctive species from Mon State and Shan State, respectively. A dichotomous key to the sixteen species of *Cyrtodactylus* known from Myanmar is presented. The discovery of seven new species of the genus suggests that each hill range, as well as isolated peaks, may be expected to harbor endemic species of geckos. The collections of the Myanmar Herpetological Survey in areas to the west of the Ayeyarwady River complement historical collections derived chiefly from areas to the south (the former Lower Burma) and to the west of the central arid zone.

Myanmar has long been recognized as a bridge region connecting the largely herpetofaunally discrete areas of peninsular India and southeast Asia (Theobald 1868). Despite early collecting activity in central and northern Burma (e.g., by Leonardo Fea, see Hallermann et al. 2002) as well as in Tenasserim (Tanintharyi Division), along the Thai border the majority of the country has remained poorly documented herpetologically (Inger 1999; Slowinski and Wüster 2000). Although its reptile fauna has been recognized as being relatively rich, it is not noted for its endemism. The recent series of expeditions conducted by the Myanmar Herpetofaunal Survey, a joint program of the Myanmar Nature and Wildlife Conservation Division, Forest Department, the California Academy of Sciences, and the Smithsonian's National Museum of Natural History, with support from the National Science Foundation, has, however, revealed a variety of new species, many apparently endemic to Myanmar (e.g., Slowinski and Wüster 2000; Bauer 2002). Among the lizards, one of the most interesting groups in this regard appears to be "bent-toed" geckos of the genus *Cyrtodactylus*.

Despite the taxonomic revision and allocation of bent-toed geckos to a number of putatively monophyletic and geographically cohesive groups by previous authors (Underwood 1954; Szczerbak and Golubev 1977, 1984, 1986; Kluge 1983), *Cyrtodactylus* remains a large and

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unwieldy group of approximately 70 species distributed from South Asia through the Indo-Australian Archipelago as far as the Solomon Islands (Bauer and Henle 1994). Kluge (1991, 1993, 2001) recognized two genera of tropical Asian bent-toed geckos: *Cyrtodactylus* and *Geckoella*, the latter occurring only in Peninsular India and Sri Lanka. This division has, however, not been uniformly accepted (e.g., Rösler 2000; Bauer 2002), and I here tentatively consider *Geckoella* as a subgenus of *Cyrtodactylus* pending a phylogenetic analysis of the group as a whole or, alternatively, evidence that *Geckoella* does not render remaining *Cyrtodactylus* paraphyletic.

Bauer (2002) reviewed the *Cyrtodactylus* of Myanmar and described two new taxa, bringing the number of species recorded for the country to ten. A record of *C. pulchellus* from Myanmar (Das and Lim 2000), however, has subsequently been revealed as unverified (I. Das, pers. commun., 28 June 2003), leaving nine *Cyrtodactylus* confirmed for the country. This includes *C. rubidus*, an Andaman Islands endemic, presumably present in the Cocos Group, the only part of the Andamans under the administration of Myanmar (*vide* Hundley 1964), and the mainland species *C. brevidactylus*, *C. consobrinoides*, *C. feae*, *C. khasiensis*, *C. oldhami*, *C. peguensis*, *C. slowinskii*, and *C. variegatus*. Bauer (2002) also signaled the existence of two additional, undescribed species based on unworked material from the Myanmar Herpetological Survey. Examination of this material, as well as specimens collected subsequently, reveals the existence of seven new species of *Cyrtodactylus* from Myanmar, for a total of 16 species. This is comparable to the 14 species now known from the much more intensively surveyed neighboring country of Thailand (Bauer et al. 2003).

## MATERIALS AND METHODS

The following measurements were taken with Brown and Sharpe Digit-cal Plus digital calipers (to the nearest 0.1 mm): snout-vent length (SVL; from tip of snout to vent), trunk length (TrunkL; distance from axilla to groin measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion), crus length (CrusL; from base of heel to knee); tail length (TailL; from vent to tip of tail), tail width (TailW; measured at widest point of tail); head length (HeadL; distance between retroarticular process of jaw and snout-tip), head width (HeadW; maximum width of head), head height (HeadH; maximum height of head, from occiput to underside of jaws), ear length (EarL; longest dimension of ear); forearm length (ForeaL; from base of palm to elbow); orbital diameter (OrbD; greatest diameter of orbit), nares to eye distance (NarEye; distance between anteriormost point of eye and nostril), snout to eye distance (SnEye; distance between anteriormost point of eye and tip of snout), eye to ear distance (EyeEar; distance from anterior edge of ear opening to posterior corner of eye), internarial distance (Internar; distance between nares), and interorbital distance (Interorb; shortest distance between left and right supraciliary scale rows). Unless otherwise stated, counts and measurements made on right side of specimens.

Scale counts and external observations of morphology were made using a Nikon SMZ-10 dissecting microscope. Preserved specimen photographs were taken with a Nikon CoolPix 990 digital camera. Radiographic observations were made using a Faxitron closed cabinet x-ray system. Comparisons were made with museum material in the collections of the California Academy of Sciences (CAS), National Museum of Natural History (USNM), Museum of Comparative Zoology (MCZ), Institut Royal des Sciences Naturelles de Belgique (IRSNB), and Chulalongkorn University Museum of Zoology (CUMZ), as well as original published descriptions and descriptions provided in broader faunal and taxonomic treatments (e.g., Annandale 1913; Smith 1935; Szczerbak and Golubev 1986; Hikida 1990; Ulber 1993; Darevsky and Szczerbak 1997; Das 1997; Das and Lim 2000; Bauer 2002; Bauer et al. 2002).

Geographic coordinates and elevation were recorded by the original collectors from a Garmin 12 GPS (datum WGS 84).

### SYSTEMATICS

#### Reptilia: Squamata: Gekkonidae

##### *Cyrtodactylus annandalei* Bauer, sp. nov.

Figs. 1–2

**HOLOTYPE.**— California Academy of Sciences (CAS) 215722 (Field number JBS 4995), adult male; Gon Nyin Bin Camp, Alaungdaw Kathapa National Park, Monywa District, Sagaing Division, Myanmar (22°14'51.1"N, 94°37'19.3"E); collected by Thin Thin, San Lwin Oo, Hla Tun, Z.T. Aung, and T.T. Soe, 6 July 2000.

**PARATYPES.**— USNM 559840 (Field number JBS 5066), adult female; Pwint Kyi Camp, Alaungdaw Kathapa National Park, Monywa District, Sagaing Division, Myanmar (22°14'39.8"N, 94°37'49.8"E); same collectors as holotype, 11 July 2000. CAS 215757 (Field number JBS 5077), adult female; Pwint Kyi Camp, Alaungdaw Kathapa National Park, Monywa District, Sagaing Division, Myanmar (22°14'39.8"N, 94°37'49.9"E); same collectors as holotype, 12 July 2000.

**ETYMOLOGY.**— The specific epithet is a patronym honoring Thomas Nelson Annandale (1876–1924), founder and director of the Zoological Survey of India. Annandale described numerous reptiles, including geckos from tropical Asia, especially India and Burma. In particular, he (Annandale 1905b) described *Gymnodactylus consobrinoides*, the species most closely resembling *C. annandalei*, from Tavoy (Tavai). The name is masculine and is formed in the genitive case.

**DEFINITION.**— A small sized *Cyrtodactylus*, snout-vent length 49–55 mm; body relatively slender, limbs, and especially digits, short; one pair of enlarged postmental scales in broad contact behind mental; dorsum relatively smooth textured, with 16–18 rows of small, keeled tubercles; 43 ventral scales across mid-body; no precloacal groove, 11–12 precloacal pores in a single series in both males and females, 10–11 femoral pores in males, separated from precloacal series by a diastema. Ten subdigital lamellae beneath 4<sup>th</sup> toe of pes distal to digital inflection. Subcaudal scalation of original tail with alternating rows forming wide transverse plates. Dorsal pattern of 6 dark bands (one each on occiput and nape, four on trunk and sacrum) or rows of transversely arranged spots, with narrow whitish borders. Dorsum of head patternless. Tail with alternating light and dark banding.

**DESCRIPTION** (based on holotype, CAS 215722).— Adult male with midventral incision from tissue removal. Snout-vent length 49.0 mm. Head relatively long (HeadL/SVL ratio 0.28), moderately wide (HeadW/HeadL



FIGURE 1. Holotype of *Cyrtodactylus annandalei*, sp. nov. (CAS 215722) from Alaungdaw Kathapa National Park, Myanmar. Note the relatively short digits, patternless head dorsum, and distinct dorsal pattern. Scale bar = 10 mm.



ratio 0.61), not depressed (HeadH/HL ratio 0.42), distinct from neck. Lores and interorbital region inflated, canthus rostralis not particularly prominent. Snout moderately short (SnEye/HeadL ratio 0.39); longer than eye diameter (OrbD/SnEye ratio 0.60); scales on snout and forehead rounded, granular, flattened to slightly conical, becoming heterogeneous posteriorly; scales on snout larger than those on occipital region. Eye small (OrbD/HeadL ratio 0.23); pupil vertical with crenelated margins; supraciliaries short, without projecting spines. Ear opening oval, moderately large (EarL/HeadL ratio 0.07); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.32). Rostral approximately half as deep (1.2 mm) as wide (2.4 mm), incompletely divided dorsally by weakly developed rostral groove; two enlarged supranasals separated by two much smaller internasals; rostral in contact with supralabial I, supranasals, and internasal; nostrils circular, each surrounded by supranasal, rostral, first supralabial, and three postnasals, rostral contact of narial border extensive; narial flap partially occludes posterior third of nostril; two to three rows of scales separate orbit from supralabials. Mental subtriangular, much wider (2.2 mm) than deep (1.6 mm); one pair of enlarged postmentals, each 60% size of mental, in broad contact with one another medially, bordered anterolaterally by first infralabial, posterolaterally by enlarged lateral chinshield, and posteriorly by 2–3 chin granules. Infralabials bordered medially by 1–3 rows of enlarged scales. Supralabials (to midorbital position) 7 (left) – 8 (right); enlarged supralabials to angle of jaws 10; infralabials 9; interorbital scale rows across narrowest point of frontal 12.

Body relatively slender, relatively short (TrunkL/SVL ratio 0.40) with ventrolateral folds indistinct. Dorsal scales small, granular, conical, with regularly arranged small tubercles extending from posterior border of orbits and temporal region on to tail base; each tubercle rounded, bearing a single prominent keel; tubercles becoming smaller and less prominently keeled on flanks; largest keeled tubercles in approximately 16 regular rows at midbody. Ventral scales much larger than dorsal, smooth, subimbricate laterally, strongly imbricate across midventer; somewhat larger than elsewhere along ventral midline of chest and abdomen, and especially in preloacal region; midbody scale rows across belly to edge of flanks (as demarcated by dorsal color pattern) 43; gular region with homogeneous scalation. Preloacal pores in a single continuous series of 11; bordered posteriorly by a row of greatly enlarged poreless scales. Femoral pores present in continuous rows of 10 (left) – 11 (right), separated from preloacal pores by a diastema of 5 scales; no preloacal groove. Scales on palm and sole smooth, rounded; scales on dorsal aspects of limbs smooth, subimbricate, heterogeneous but without tubercles.

Fore- and hindlimbs relatively short, stout; forearm short (ForeaL/SVL ratio 0.14); tibia moderate (CrusL/SVL ratio 0.17); digits short, strongly inflected at basal interphalangeal joints, all bearing robust, slightly recurved claws; subdigital lamellae rounded, smooth, without scansorial surfaces; lamellae distal to much enlarged scale at basal digital inflection and not including ventral claw sheath: 6–7–8–8–8 (manus), 8–8–10–10–10 (pes), proximal 1–2 fragmented on most digits; enlarged basal lamellae ( $\geq$  twice size of palmar scales) to and including enlarged scale at basal inflection: 3–4–5–5–4 (manus), 3–5–6–7–5 (pes); interdigital webbing absent. Relative length of digits (manus; measurements in mm in parentheses): III (3.4)  $\simeq$  IV (3.4)  $>$  V (2.7)  $\simeq$  II (2.6)  $>$  I (2.4); (pes): IV (4.5)  $>$  V (4.2)  $>$  III (3.8)  $>$  II (3.3)  $>$  I (2.3).

Tail original, slightly longer than body (TailL/SVL ratio 1.04), slender, tapering; divided into indistinct segments, each approximately 7 dorsal scale rows in length; two rows of enlarged, keeled tubercles positioned paravertebrally on tail base only, remaining dorsal caudal scales small, smooth, rectangular; subcaudal scales larger, smooth, imbricate; subequal basally, distally with alternating midventral scales enlarged into transverse plates. Two enlarged, smooth, conical postloacal spurs on each side of tailbase.

Osteology. Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for



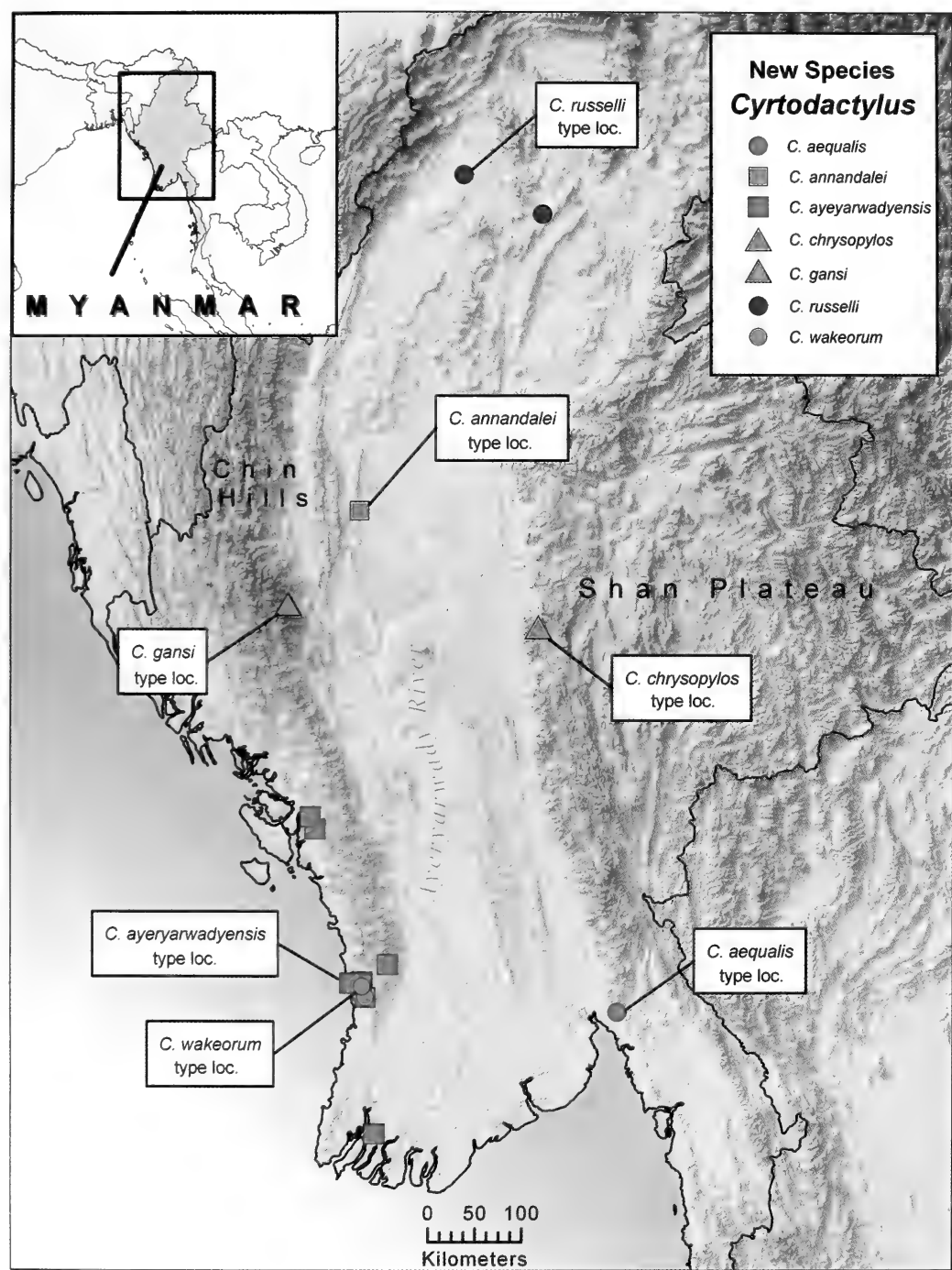


FIGURE 3. Map of Myanmar illustrating the distribution of seven new species of *Cyrtodactylus*: *C. aequalis* (red circle), *C. annandalei* (yellow square), *C. ayeyarwadyensis* (red square), *C. chrysopylos* (yellow triangle), *C. gansi* (green triangle), *C. russelli* (blue circle), and *C. wakeorum* (yellow circle). Map prepared by Michelle S. Koo, California Academy of Sciences.

manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 32 post pygal caudal vertebrae in original tail in holotype (32 in larger paratype; 5.5 in smaller paratype with regenerate tail). One pair of slender, crescentic cloacal bones in male holotype (absent in female paratypes). Endolymphatic sacs not enlarged extracranially. Subadult female with significant areas of incomplete ossification at joints of long bones.

Coloration (in preservative). Base color a pale brown. Boldly marked with chocolate brown bands, each outlined by a thin cream to whitish border 1–2 scale widths in thickness. Occipital band extending anteriorly to orbit and under eye to loreal region; continues indistinctly to rostral. Dorsum of head patternless. Nuchal collar extending anteriorly to posterior border of ear. Four additional bands between shoulders and sacrum. Ventrolateral pale brown spaces between body bands with large, chocolate brown spots. Pattern bilaterally symmetrical on head and nape, somewhat asymmetrical more posteriorly. Forelimbs mottled, with an indistinct dark line along preaxial surface of humerus; hindlimbs boldly marked with spots and oblong markings like those on flanks. Hindlimb insertions with large chocolate brown blotches at posterior border of thighs. Venter cream tinged by the light brown speckling of individual scales. Tail mottled gray-brown with darker irregular transverse markings, except on enlarged imbricate median scales. Tail with alternating chocolate brown and light brown to cream banding. Paler bands wider than darker, 12 dark bands from cloaca to tail tip. Tail venter with scattered dark pigmentation, especially distally. Dorsal color pattern extends onto ventrum only at tail tip.

In life, dorsum distinctly darker than flanks. Pale borders of dark spots yellowish-cream (Fig. 2).

**VARIATION.**—Comparative mensural data for the holotype and paratypes are presented in Table 1. Both paratypes similar to holotype in most respects except as noted. CAS 215757: adult female with midventral incision from tissue removal. 18 rows of keeled tubercles across midbody. 12 tiny precloacal pores and 4 (left) and 10 (right) weakly developed femoral pores. Nuchal collar fragmented anteriorly; dark markings present above forelimb insertions, diffuse dark line absent from preaxial border of humerus; 11 dark bands on original tail. CAS 215749: subadult female with midventral incision from tissue removal. 18 rows of keeled tubercles across midbody. Broken row of 8 tiny precloacal pores and 7 weakly developed femoral pores on each side. Dorsal pattern highly fragmented into spots rather than bands; 4 spots in a transverse row representing each posterior body band; hindlimbs with only a few small spots; infralabials brownish; regenerated tail mottled, without banding.

**DIAGNOSIS.**—*Cyrtodactylus annandalei* may be distinguished from all congeners on the basis of its relatively short digits, series of 8–12 precloacal pores separated by a diastema from 4–12 femoral pores on each thigh, no precloacal groove or enlarged femoral scales, dorsal tubercles small, in 16–18 longitudinal rows, ventral scales in 43 rows, alternate subcaudal scales enlarged transversely, and dorsal color pattern, including occipital, nape, and four additional dark body bands (or series of spots), and patternless head dorsum.

The new species is superficially most similar to *C. consobrinoides* (Annandale, 1905a;



FIGURE 2. Living specimen (paratype) of *Cyrtodactylus annandalei* (CAS 215757). Photo by Hla Tun.

TABLE 1. Mensural data for the type series of *Cyrtodactylus annandalei*, sp. nov. Abbreviations as in Materials and Methods section; all measurements in mm.

	CAS 215722 <i>Holotype</i>	CAS 215757 <i>paratype</i>	CAS 215749 <i>paratype</i>
<i>Sex</i>	male	female	female
<i>SVL</i>	49	55.3	51.1
<i>ForeaL</i>	7	8.2	6.7
<i>CrusL</i>	8.4	9.5	8.6
<i>TailL (entire)</i>	50.8	55.5	36.4
<i>TailL (portion regenerated)</i>	—	—	22.8
<i>TailW</i>	4	5.4	4.3
<i>TrunkL</i>	19.7	22.6	22.9
<i>HeadL</i>	13.5	16.2	13.8
<i>HeadW</i>	8.3	9.4	8.1
<i>HeadH</i>	5.6	6	4.7
<i>OrbD</i>	3.2	3.5	3.2
<i>EyeEar</i>	4.2	4.6	3.9
<i>SnEye</i>	5.3	5.6	5.2
<i>NarEye</i>	3.6	3.9	3.3
<i>Interorb</i>	5.5	5.2	4.5
<i>EarL</i>	1	1.3	1.3
<i>Internar</i>	2.2	2	1.9

Annandale 1905b), from which it differs in having a smaller number of thicker dark crossbands (6–7 vs. 8–9), no enlarged femoral scales, femoral pores present and separated from precloacal scales by a diastema, a larger number of ventral scale rows (43 vs. 20–30, although this count is somewhat arbitrary in the absence of ventrolateral folds as lateral landmarks for such counts), and a patternless head dorsum. It also lacks the light borders around the dorsal markings illustrated by Annandale (1913) in his redescription of the holotype of *C. consobrinoides*. A specimen from Molmein (Mawlamyine), provisionally referred to *C. consobrinoides* by Smith (1935) has 40 ventral scale rows and only six dorsal bands and may be referable to *C. annandalei*, although the huge distance (ca. 680 km) between Mawlamyine and the type locality make this unlikely. Comparisons with other species are provided following the description of all new taxa.

**DISTRIBUTION.**— *Cyrtodactylus annandalei* is known only from Alaungdaw Kathapa National Park in the Sagaing Division of north central Myanmar (Fig. 3). The most similar species to this form, *C. consobrinoides* is known only from southern Myanmar, with records from Tavoy (Dawei, Tanintharyi State) (Annandale 1905a, 1905b, 1913) and Molmein (Mawlamyine, Mon State) (Smith 1935; but see above). The species is sympatric with the much larger and recently described *C. slowinskii* as well as an unidentified species related to *C. khasiensis* (USNM 548140). The type locality is in the central dry zone of Myanmar, between the Rakhine Yoma (Arakan Yoma) of the Indo-Burman Range in the west and the extensive montane areas east of the Sittaung River.

*Cyrtodactylus ayeeyarwadyensis* **Bauer, sp. nov.**  
Figs. 4–6

**HOLOTYPE.**— CAS 226154 (Field number JBS 8689), adult male; Khoko Gwe Creek,

Rakhine Yoma Elephant Range, Gwa Township, Rakhine State, Myanmar ( $17^{\circ}43'48.3''\text{N}$ ,  $94^{\circ}39'02.7''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Kyi Soe Lwin and Hla Tun, 28 April 2001.

**PARATYPES** (8 specimens).—CAS 226153 (Field number JBS 8688), adult male; same data as for holotype. CAS 226147 (Field number JBS 8346), adult female; Kanthaya, Gwa Township, Rakhine State, Myanmar ( $17^{\circ}43'24.9''\text{N}$ ,  $94^{\circ}32'08.3''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 22 April 2001. CAS 226149 (Field number JBS 8519), adult male; Kyat Stream, Rakhine Yoma Elephant Range, Gwa Township, Rakhine State, Myanmar ( $17^{\circ}42'14.0''\text{N}$ ,  $94^{\circ}38'54.3''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 26 April 2001. USNM 559837 (Field number JBS 8635), adult male; locality and collectors as for CAS 226149, 27 April 2001. CAS 226152 (Field number JBS 8638), adult female; data as for CAS 226150; USNM 559838 (Field number JBS 8637), adult female; data as for CAS 226150. CAS 226156 (Field number JBS 8782), adult female; Kanthaya, Gwa Township, Rakhine State, Myanmar ( $17^{\circ}43'14.6''\text{N}$ ,  $94^{\circ}32'04.9''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 2 May 2001. CAS 216506 (Field number JBS 7467), adult male; Elephant Camp, Rakhine Yoma Elephant Range, Gwa Township, Than Dawe District, Rakhine State, Myanmar ( $17^{\circ}39'01.1''\text{N}$ ,  $94^{\circ}38'39.2''\text{E}$ ); collected by J.B. Slowinski and Htun Win, 30 November 2000.

**ADDITIONAL MATERIAL** (16 specimens).—All specimens from Myanmar. CAS 226146 (Field number JBS 8342); Kanthaya, Gwa Township, Rakhine State ( $17^{\circ}43'24.9''\text{N}$ ,  $94^{\circ}32'08.3''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 22 April 2001. CAS 226151 (Field number JBS 8636); Kyat Stream, Rakhine Yoma Elephant Range, Gwa Township, Rakhine State ( $17^{\circ}42'14.0''\text{N}$ ,  $94^{\circ}38'54.3''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 27 April 2001. CAS 221934 (Field number JBS 8946); Rakhine Yoma Elephant Range, Gwa, Gwa Township, Rakhine State ( $17^{\circ}35'02.4''\text{N}$ ,  $94^{\circ}40'44.2''\text{E}$ ); collected by Htun Win, Thin Thin, Kyi Soe Lwin and Awan Khwi Shein, 2 June 2001. CAS 221985 (Field number JBS 9296); Kyauk Win Gyi Camp, Gwa Township, Rakhine State ( $17^{\circ}53'59.9''\text{N}$ ,  $94^{\circ}53'36.8''\text{E}$ ); collected by Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 9 June 2001. CAS 226155 (Field number JBS 8781), CAS 226157 (Field number JBS 8783), CAS 226158–226159 (Field numbers JBS 8792, 8794); Kanthaya, Gwa Township, Rakhine State ( $17^{\circ}43'14.6''\text{N}$ ,  $94^{\circ}32'04.9''\text{E}$ ); collected by J.B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 2 May 2001. CAS 216526 (Field number JBS 7496); Elephant Camp, Rakhine Yoma Elephant Range, Gwa Township, Than Dawe District, Rakhine State ( $17^{\circ}38'58.3''\text{N}$ ,  $94^{\circ}38'14.8''\text{E}$ ); collected by J.B. Slowinski and Htun Win, 1 December 2000. CAS 216446 (Field number JBS 7363); vicinity of Kanthaya Beach, Gwa Township, Rakhine State (no coordinates recorded); collected by J.B. Slowinski and Htun Win, 27 November 2000. CAS 212459 (Field number JBS 4647); vicinity of Mwe Hauk Village, Myaung Mya Township, Ayeyarwady Division ( $16^{\circ}16'29.4''\text{N}$ ,  $94^{\circ}46'04.0''\text{E}$ ); collected by J.B. Slowinski, G.R. Zug, R.S. Lucas and J.V. Vindum, 22 April 2000. CAS 222812 (Field number JBS 11012); Mwe Hauk Village, Myaung Mya Township, Ayeyarwady Division ( $16^{\circ}16'34.8''\text{N}$ ,  $94^{\circ}45'46.8''\text{E}$ ); collected by G.O.U. Wogan, Htun Win, Awan Khwi Shein, Kyi Soe Lwin and Hla Tun, 20 January 2002.

In addition, the following specimens, although differing in minor aspects of coloration from the types of *C. ayeyarwadyensis*, appear to be referable to this species. Further collecting in intervening areas, however, may necessitate the reevaluation of these northern populations: CAS 223044 (Field number JBS 11324); Sa Byin Village, Taung Gok Township, Rakhine State

(19°11'56.1"N, 94°11'56.1"E, 61 ft.); collected by G.O.U. Wogan, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 27 January 2002. CAS 223285 (Field number JBS 11691); Tha Byut Stream, Ma Ei Ywa Ma Village, Taung Gok Township, Rakhine State (19°18'51.0"N, 94°09'06.5"E); collected by G.O.U. Wogan, R.S. Lucas, Htun Win, Awan Khwi Shein and Kyi Soe Lwin, 2 February 2002. CAS 223289 (Field number JBS 11698); Tha Byut Stream, Ma Ei Ywa Ma Village, Taung Gok Township, Rakhine State (19°18'49.2"N, 94°09'08.8"E); collected by G.O.U. Wogan, R.S. Lucas, Htun Win, Awan Khwi Shein and Kyi Soe Lwin, 2 February 2002. CAS 223339 (Field number JBS 11724); Tha Byut Stream, Ma Ei Ywa Ma Village, Taung Gok Township, Rakhine State (19°18'51.7"N, 94°09'07.8"E); collected by G.O.U. Wogan, R.S. Lucas, Htun Win, Awan Khwi Shein and Kyi Soe Lwin, 2 February 2002.

**ETYMOLOGY.**— The specific epithet is derived from the Ayeyarwady (Irrawaddy) River which runs through Myanmar. The range of the species includes parts of the Ayeyarwady delta.

**DEFINITION.**— A moderate sized *Cyrtodactylus*, snout-vent length to 78 mm; body relatively slender, limbs moderately long and digits relatively short; one pair of enlarged postmental scales, in broad contact with one another behind mental; 22–24 rows of keeled, oblong dorsal tubercles; 32–37 ventral scales between ventrolateral folds; no precloacal groove, 10–28 precloacal pores in a single series (or with scattered gaps of one poreless scale) in males only. Six widened subdigital lamellae beneath basal phalanx of 4<sup>th</sup> toe of pes, 10 narrow lamellae beneath more distal phalanges of same toe (in holotype). Subcaudal scalation without enlarged midventral plates. Dorsal pattern of 9–11 (usually 10) transverse rows of rectangular brown blotches from occiput to sacrum. Posterior border of each row usually marked by white punctations or a narrow white band; tail with alternating brown and white bands.

**DESCRIPTION** (based on holotype, CAS 226154).— Adult male, SVL 63.4 mm. Head moderately long (HeadL/SVL ratio 0.28), relatively wide (HeadW/HeadL ratio 0.61), somewhat depressed (HeadH/HeadL ratio 0.35), distinct from neck. Lores and interorbital region weakly inflated, canthus rostralis not well developed. Snout moderately long (SnEye/HeadL ratio 0.41); much longer than eye diameter (OrbD/SnEye ratio 0.55); scales on snout and forehead rounded, granular, intermixed with scattered small tubercles posteriorly; scales on snout much larger than those on occipital region. Eye small (OrbD/HeadL ratio 0.22); pupil vertical with crenelated margins; supraciliaries short, blunt. Ear opening oval, obliquely oriented, large (EarL/HeadL ratio 0.09); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.21). Rostral approximately 55% as deep (1.5 mm) as wide (2.8 mm), divided dorsally by rostral groove; two enlarged supranasals separated by a single, somewhat smaller, roughly hexagonal internasal; rostral in contact with supralabial I, supranasals, and internasal; nostrils oval, laterally oriented, each in broad contact with rostral and also surrounded by supranasal, first supralabial, and three postnasals; pigmented narial flap partially occludes posterior 2/3 of nostril; 3–4 rows of scales

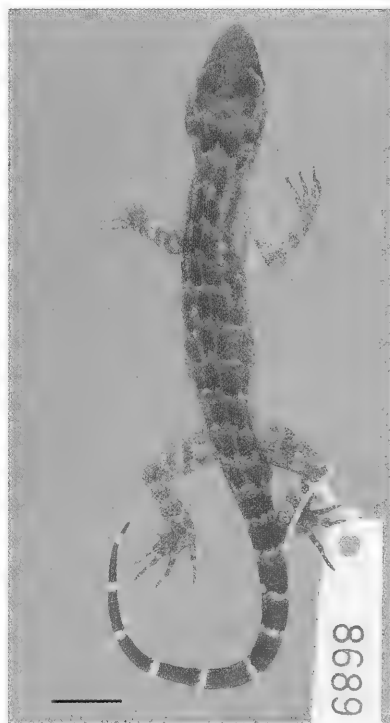


FIGURE 4. Holotype of *Cyrtodactylus ayeyarwadyensis*, sp. nov. (CAS 226154) from Rakhine Yoma Elephant Range, Gwa Township, Rakhine State, Myanmar. Note the relatively short digits, paired rectangular dorsal markings and white punctuations. Scale bar = 10 mm.

separate orbit from supralabials. Mental triangular, wider (2.8 mm) than deep (2.0 mm); one pair of greatly enlarged postmentals, each approximately 30–35% size of mental; left and right postmentals in broad medial contact with no intervening granules, each member of pair bordered laterally by first infralabial and an enlarged lateral chinshield, the pair bordered posteriorly by 5 somewhat enlarged chin scales. Infralabials bordered by 1–3 rows of enlarged scales, largest anteriorly and laterally. Throat scales small, rounded, granular. Supralabials (to midorbital position) 8 (left) – 10 (right); enlarged supralabials to angle of jaws 12 (left)–11 (right); infralabials 10; interorbital scale rows across narrowest point of frontal bone 17.

Body moderately slender, relatively short (TrunkL/SVL ratio 0.40) with very weakly denticulate ventrolateral folds. Dorsal scales heterogeneous, mostly rounded to weakly conical granules with pitted or rugose surfaces, intermixed with regularly arranged small (4–6 times granule size), keeled, oblong tubercles extending from occipital region on to back and base of tail; tubercles on nape more strongly conical and without keels; tubercles in approximately 22 longitudinal rows at midbody; 50 tubercles in paravertebral row from occiput to mid sacrum. Ventral scales much larger than dorsal, cycloid, imbricate to subimbricate; not enlarged under thighs or between precloacal pores and vent; midbody scale rows across belly between ventrolateral folds 34; scales on throat minute, granular, grading into larger scales on chest. Precloacal pores in a single series of 21, with a gap of one poreless scale separating the distalmost two pores of the right side; no femoral pores; no precloacal groove. Scales on palm and sole smooth, flattened; scales on dorsal aspects of hindlimbs granular, conical, similar to dorsal scales, with larger, conical tubercles interspersed. Dorsal scales of proximal forelimbs imbricate, without tubercles; scales of forearms heterogeneous with scattered conical tubercles.

Fore and hindlimbs relatively slender; forearm (ForeaL/SVL ratio 0.16) and tibia (CrusL/SVL ratio 0.18) relatively long; digits relatively short, strongly inflected at each joint, all bearing robust, recurved claws; subdigital lamellae widened beneath basal phalanx; lamellae from first proximal scansor greater than twice largest palm scale to basalmost digital inflection: 4–5–5–5–4 (manus) and 3–5–5–6–5 (pes); lamellae from basalmost digital inflection to toe tip, not including ventral claw sheath: 7–8–8–7–7 (manus) and 7–10–8–10–10 (pes); one to several rows of small, non-lamellar granules between basal and distal lamellar series; interdigital webbing present but weakly developed. Relative length of digits (manus; measurements in mm in parentheses): IV (5.5) > III (5.4) > II (4.7) > V (4.6) > I (3.5); (pes): V (7.0) > IV (6.6) > III (5.4) > II (5.0) > I (2.8).

Original tail longer than body (TailL/SVL ratio 1.11), slender, cylindrical in cross section. Scales arranged in regular segments; ventral scales rectangular, dorsal scales rounded at free margins. Eight circumferential rows per segment; basal segment with one row of 6 enlarged keeled tubercles, each tubercle separated from next by 1–4 smaller scales; more distally tubercles are unkeeled; tubercles absent on distal 3/4 of tail; posteriormost caudal scales narrow and elongate. Subcaudal scales larger, 6 rows per segment; segments not strongly demarcated ventrally or posteriorly; no enlarged median plates. Cloacal spurs with 3 enlarged, smooth, rounded scales on each side of tail base.

Osteology. Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 32 post pygal caudal vertebrae in original tail in holotype (32–34 in paratypes with complete tails, 0.5–21.5 in those with regenerated tails). One pair of slender, crescentic cloacal bones in males at level of first to second pygal vertebrae (absent in females). Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative). Base color a medium brown marked by 10 transverse rows of roughly rectangular dark brown patches from occiput to sacrum, each row consisting of a pair of

bold paravertebral markings and a pair of less well defined lateral markings. Each marking bolder and more well-defined posteriorly and more diffuse anteriorly. Occipital markings fused to form a complete band. Posterior border of each transverse row of rectangular patches marked by a series of tiny white punctuations, each one to several scales in extent. Top of head medium brown with a diffuse set of dark brown marks forming a semicircle between posterodorsal corners of orbits. Canthal region crossed by a diffuse dark bar. A brown streak, bordered above and below by white punctuations. White punctuations also scattered from insertion of forelimb to corner of mouth and along lower flanks. Limbs more-or-less strongly barred, with alternating light and dark markings extending on to digits, lighter bands with scattered white punctuations. Paravertebral marks fusing on tail base to form complete dark bars, 12 such bands along length of tail, including tail tip. First four bands bordered posteriorly by white punctuations and alternating with narrower light bands. More posteriorly wide dark bands alternate with continuous narrow white bands. Tail patterning extends on to venter, but bands weakly demarcated anteriorly. Venter beige with scattered dark pigment on all surfaces, darkest at lateral margins of flanks, on neck, limbs, and around cloaca. Palms and soles of feet dark.

Color in life similar to that in preservative but with medium brown of body ranging from straw to pinkish brown in some specimens. Venter white with a pale pinkish suffusion on flanks. Iris olive to greenish-gold. (Figs. 5–6)

**VARIATION.**—Comparative mensural data for the holotype and paratypes are presented in Table 2. Paratypes similar to holotype in most respects except as noted. Scale rows between ventrolateral folds at midbody 32–37. Rows of dorsal tubercles at midbody 22–24. Precloacal pores 10–28, generally continuous, but with a single poreless scale dividing the series into 24 (left) and 4 (right) pored scales in CAS 216506; pores absent in females. First supralabial scales excluded from nostril in some specimens (CAS 216506, CAS 226156), nostril contacted by one postnasal and a large crescentic nasal (CAS 216506, 226147, 226149, 226152), two postnasals and a crescentic nasal (CAS 226156, USNM JBS 8637), or by an asymmetrical number of postnasals (3 left, 4 right in CAS 226150, 4 left, 5 right in 226153). The largest of the paratypes, CAS 226152, is a gravid female with two eggs clearly visible through the abdominal wall. Among the additional specimens referred to *C. ayeyarwadyensis*, sizes range from 34.4 mm (CAS 212459, juvenile) to 78.3 mm (CAS 221985, adult female).

Color pattern highly variable. Among the paratype series the number of pairs of dorsal markings was 10, as in the holotype, for most specimens, but ranged from 9 (CAS 216506, 226150, 226156) to 11 (CAS 226147). These markings may be evenly paired or partly phase shifted between the left and right sides of the animal. The dark dorsal markings are especially strongly contrasting with respect to background color in CAS 216506 and 226149. The white punctuations may



FIGURE 5. Living specimen of *Cyrtodactylus ayeyarwadyensis*, sp. nov. (CAS 226158) illustrating life coloration. Photo by Hla Tun.



FIGURE 6. Head and forebody of living paratype of *Cyrtodactylus ayeyarwadyensis*, sp. nov. (CAS 216506) illustrating greenish iris and the relatively short, kinked digits of the manus. Photo by Hla Tun.

TABLE 2. Mensural and meristic data for the type series of *Cyrtodactylus ayeyarwadyensis*, sp. nov.  
Abbreviations as in Materials and Methods section; all measurements in mm.

	CAS 226154 Holotype	CAS 216506 Paratype	CAS 226147 Paratype	USNM JBS8637 Paratype	CAS 226156 Paratype	CAS 226149 Paratype	CAS 226150 Paratype	CAS 226153 Paratype	CAS 226152 Paratype
Sex	male	male	female	female	female	male	male	male	female
SVL	63.4	67.6	64.1	65.9	65.5	66.6	62.1	65.4	71.8
ForeaL	9.8	10	9.4	9.8	9.5	10.1	9.9	9.6	11.8
CrusL	11.6	12	11.5	11.7	12.1	12.3	11.5	10.7	13.1
TailL (total)	70.1	53.2	64.6	73.3	70.7	73.7	71	71.5	6.1
TailL (regen)	—	43.3	13	—	—	—	—	25.5	(broken)
TailW	6.9	6.3	5.3	5.4	5.4	5.6	5.7	5.8	6.8
TrunkL	25.5	28.5	28.8	29	28	27.7	28.3	26.7	34.2
HeadL	18	18.5	18.8	18.1	19	18.9	17.1	18.6	20.7
HeadW	11	12.5	11.9	11.6	11.3	11.1	11.2	11.4	12.8
HeadH	6.3	6.8	6.4	6.9	7.3	6.9	6.3	6.9	8.5
OrbD	4	4.8	4.1	4.6	4.9	4.6	4.2	4.4	5
EyeEar	4.9	5.4	4.8	5.4	5.3	5	4.7	4.6	5.5
SnEye	7.3	7.6	7	6.9	7.4	7.3	7	7	8.2
NarEye	5.1	4.8	4.9	5	4.9	5.1	4.5	4.9	5.8
Interorb	6.2	6.9	5.8	6.5	6.4	6.2	5	7.1	7.6
EarL	1.6	2.1	2.1	1.6	1.6	1.9	1.8	2.3	2.1
Internar	2	2.1	2.4	1.7	2	1.8	1.8	1.9	2.1
Tubercle Rows	22	24	22	22	22	22	22	24	22
Ventral Scale Rows	34	34	34	36	34	37	34	32	36
Precloacal Pores	21	28	—	—	—	13	10	10	—

be greatly reduced or lacking almost all together (CAS 216506). Among the additional material referred to this taxon pattern was even more variable, with several specimens from Rakhine State (CAS 223285, 223289, 223339) with the white markings coalescent, forming distinct transverse bands.

**DIAGNOSIS.**— *Cyrtodactylus ayeyarwadyensis* may be distinguished from all congeners on the basis of its possession of short digits, a single series of precloacal pores (10–28) in males only, absence of femoral pores and precloacal groove, 22–24 longitudinal rows of dorsal tubercles; 32–37 ventral scales between ventrolateral folds, subcaudal scalation without enlarged midventral plates, and dorsal pattern of 9–11 (usually 10) transverse rows of rectangular brown blotches from occiput to sacrum, usually bordered posteriorly by white punctations or a narrow white band.

Among other species from Myanmar it is most similar to *C. khasiensis* and a new species from Chin State, described below. All are similar in size and bear a series of dark dorsal markings. *Cyrtodactylus ayeyarwadyensis* differs from *C. khasiensis*, however, in having (in some specimens) a greater number of precloacal pores (maximum 28 vs 14), rectangular dorsal blotches (vs a more variegated pattern of alternating irregular light and dark bands, or even stripes; Hora 1926), white dorsal punctuations or lines bordering dorsal blotches (in most cases), and narrow white tail



bands (vs subequal light and dark bands in *C. khasiensis*). It differs from the other new species in both color pattern (rectangular dark markings and white punctuations vs narrow transverse bands) and precloacal pore configuration (strongly angled and recessed into a shallow groove in the Chin State species). Comparisons with other species are provided after the new species descriptions.

**DISTRIBUTION.**— Typical specimens of *Cyrtodactylus ayeyarwadyensis* are known from low elevation in extreme southwestern Myanmar, west of the main channel of the Ayeyarwady (Irrawaddy) River, specifically from Gwa Township in Rakhine State and Myaung Mya Township in the Ayeyarwady Division. Additional specimens tentatively referred to *C. ayeyarwadyensis* derive from Taung Gok Township, Rakhine State. This locality is considerably north of the Ayeyarwady delta, but is also low-lying, to the west of the southern chain of the Rakhine Yoma (Arakan Yoma) (Fig. 3).

*Cyrtodactylus gansi* Bauer, sp. nov.

Figs. 7–9

**HOLOTYPE.**— CAS 222414 (Field number JBS 8300); Che Stream, Min Dat Township, Min Dat District, Chin State (21°21'15.5"N, 93°56'13.3"E, 780 m.); collected by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 3 April 2001.

**PARATYPES.**— CAS 222411 (Field number JBS 8234); Che Stream, Min Dat Township, Min Dat District, Chin State (21°21'14.9"N, 93°56'08.3"E, 750 m.); collected by Awan Khwi Shein, 29 March 2001. USNM 559839 (Field number JBS 8258), CAS 226145 (Field number JBS 8260); same locality as CAS 222411; collected by Htun Win, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 31 March 2001. CAS 222412–222413 (Field numbers JBS 8240–41); Che Stream, Min Dat Township, Min Dat District, Chin State (21°21'14.9"N, 93°56'08.3"E, 1298 m.); collected by Htun Win, Thin Thin, Kyi Soe Lwin and Awan Khwi Shein, 30 March 2001.

**ETYMOLOGY.**— The specific epithet is a patronym honoring Carl Gans (born 1923), who has made substantial contributions to the herpetology of tropical Asia and who has been a strong influence on my own professional career and that of many other herpetologists and vertebrate morphologists around the world. The name is masculine and is formed in the genitive case.

**DEFINITION.**— A moderate sized *Cyrtodactylus*, snout-vent length to 63 mm; body relatively slender, limbs and digits relatively short; one pair of enlarged postmental scales, in broad contact with one another behind mental; 20–25 rows of rounded, conical dorsal tubercles; 36–40 ventral scales between lowest rows of dorsal tubercles; no discrete ventrolateral folds; shallow precloacal groove in males, 16–29 large precloacal pores in a single, strongly angled series (pores smaller and not recessed in females). Seven widened subdigital lamellae beneath basal phalanx of 4<sup>th</sup> toe of pes, 11 narrow lamellae beneath more distal phalanges of same toe (in holotype). Subcaudal scalation without enlarged midventral plates. Dorsal pattern of approximately 10 narrow, dark brown transverse bands from occiput to sacrum. Tail with alternating brown and white bands.

**DESCRIPTION** (based on holotype, CAS 222414).— Adult male, SVL 60.8 mm. Head moderately long (HeadL/SVL ratio 0.28), relatively narrow (HeadW/HeadL ratio 0.58), not depressed (HeadH/HeadL ratio 0.40), distinct from neck. Lores and interorbital region inflated, canthus rostralis not well developed. Snout short (SnEye/HeadL ratio 0.36); much longer than eye diameter (OrbD/SnEye ratio 0.66); scales on snout and forehead rounded, granular to weakly conical, intermixed with scattered small tubercles behind level of orbits; scales on snout much larger than those on occipital region. Eye relatively small (OrbD/HeadL ratio 0.24); pupil vertical with crenelated margins; supraciliaries short, blunt. Ear opening round, moderately large (EarL/HeadL ratio 0.07); eye to ear approximately equal to diameter of eyes (EyeEar/OrbD ratio 1.03). Rostral approximately 75% as deep (1.9 mm) as wide (2.5 mm), divided dorsally by rostral groove; two enlarged



FIGURE 7. Holotype of *Cyrtodactylus gansi*, sp. nov. (CAS 222414) from Min Dat Township, Chin State, Myanmar. Note the relatively short digits, narrow dark crossbands, and lack of transverse rows of white punctations. Scale bar = 10 mm.

Dorsal scales of proximal forelimbs imbricate, without tubercles; scales of forearms heterogeneous with few scattered conical tubercles.

Fore- and hindlimbs relatively slender; forearm (ForeaL/SVL ratio 0.15) and tibia (CrusL/SVL ratio 0.17) moderate in length; digits relatively short, strongly inflected at each joint, all bearing robust, recurved claws; subdigital lamellae widened beneath basal phalanx to approximately half digital width; lamellae from first proximal scansor greater than twice

supranasals separated by a single, somewhat smaller, anterior internasal and two much smaller posterior internasals; rostral in contact with supralabial I, supranasals, and anterior internasal; nostrils oval, laterally oriented, each in broad contact with rostral and also surrounded by supranasal, first supralabial, and two postnasals; pigmented narial flap partially occludes posterior half of nostril; 2–5 rows of scales separate orbit from supralabials. Mental triangular, wider (2.3 mm) than deep (1.6 mm); one pair of greatly enlarged postmentals, each approximately 40% size of mental; left and right postmentals in broad medial contact with no intervening granules, each member of pair bordered laterally by first infralabial and an enlarged lateral chinshield, the pair bordered posteriorly by 7 slightly enlarged chin scales. Infralabials bordered by 2–3 rows of enlarged scales, largest anteriorly and laterally. Throat scales small, rounded, granular. Supralabials (to midorbital position) 8; enlarged supralabials to angle of jaws 11 (left)–12 (right); infralabials 11; interorbital scale rows across narrowest point of frontal bone 13.

Body moderately slender, elongate (TrunkL/SVL ratio 0.46) without discrete ventrolateral folds. Dorsal scales heterogeneous, mostly rounded to weakly conical granules with pitted or rugose surfaces, intermixed with regularly arranged small (3 times granule size), rounded, conical tubercles extending from occipital region on to back and base of tail; tubercles on nape smaller than those on body dorsum; tubercles in approximately 22 longitudinal rows at midbody; 53 tubercles in paravertebral row from occiput to mid sacrum. Ventral scales much larger than dorsal, cycloid, imbricate to subimbricate; enlarged between precloacal pores and vent; midbody scale rows across belly between lowest rows of dorsal tubercles 36; scales on throat minute, granular, grading into larger scales on chest. Precloacal pores large, in a single, strongly angled series of 17 lying in a shallow precloacal groove (Fig. 8); no femoral pores. Scales on palm and sole smooth, flattened; scales on dorsal aspects of hindlimbs granular, conical, similar to dorsal scales, with larger, conical tubercles interspersed.

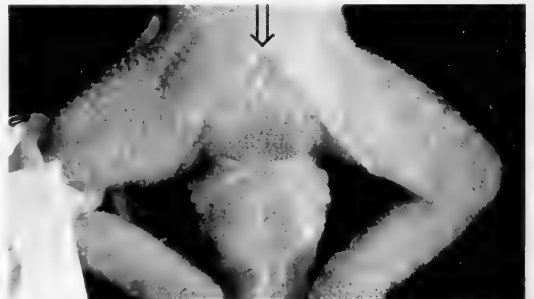


FIGURE 8. Cloacal region of holotype of *Cyrtodactylus gansi*, sp. nov. (CAS 222414). Note the strongly angled and shallowly recessed series of large precloacal pores and the enlarged row of scales posterior to the pore-bearing scales. Arrow indicates apex of pore-bearing scale series.

largest palm scale to basalmost digital inflection: 3–4–5–6–3 (manus) and 2–5–6–7–5 (pes); lamellae from basalmost digital inflection to toe tip, not including ventral claw sheath: 7–8–10–10–9 (manus) and 8–9–11–11–11 (pes); one to several rows of small, non-lamellar granules between basal and distal lamellar series; interdigital webbing present but weakly developed. Relative length of digits (manus; measurements in mm in parentheses): IV (5.1) > III (4.8) > II (4.3) > V (4.0) > I (2.5); (pes): IV (6.2) > V (5.8) > III (5.6) > II (4.8) > I (2.8).

Partially regenerated tail longer than body (TailL/SVL ratio 1.24), slender, cylindrical in cross section. Scales arranged in regular segments; dorsal and ventral scales rounded at free margins. Eight circumferential rows per segment; pygal segments with one transverse row of 12 enlarged conical tubercles, each tubercle separated from next by 2–5 smaller scales; more distally tubercles decreasing to 6 then 2 per segment; tubercles absent on distal 3/4 of tail; posteriormost caudal scales narrow and elongate. Subcaudal scales much larger than dorsal, 3 rows per segment; no enlarged median plates. Cloacal spurs with 3 enlarged, smooth, flattened, pointed scales on each side of tail base.

Osteology. Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 17.5 postpygal caudal vertebrae in the partly regenerated tail in holotype (31–34 in paratypes with complete tails, 1.5 in paratype with broken tail). One pair of slender, crescentic cloacal bones, with enlarged lateral flanges present in males at level of second pygal vertebrae (absent in female paratype). Cloacal bones relatively large in all males except subadult paratype (CAS 222411), which exhibits incomplete ossification of some long bones (juvenile paratype not examined osteologically). Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative). Base color light to medium brown with dark transverse markings, irregular from nape to shoulder, forming 7 more-or-less continuous crossbands from forelimb insertion to sacrum. Bands terminate abruptly on flanks; small, dark spots irregularly positioned at ventrolateral margins, between ends of crossbands. Top of head medium brown with a diffuse set of irregular dark brown spots. Canthal region somewhat darker than rest of snout. A brown streak running from behind orbit to above ear, in conjunction with dark spots on neck forming a broken nape band. Limbs and feet bearing dark spots. Dark markings on tail forming 10 bands, some partly fused with one another, on original portion of tail. Dark tail bands slightly narrower than lighter interstices. Tail patterning does not extend on to venter. Venter beige with scattered dark pigment on all surfaces, darkest under thighs and around cloaca. Palms and soles of feet darker than remainder of venter.

Color in life similar to that in preservative but rims of orbit and lateral tubercles yellow, with a yellowish tinge to the lighter areas of the limbs (Fig. 9).

**VARIATION.**—Comparative mensural data for the holotype and paratypes are presented in Table 3. Paratypes similar to holotype in most respects except as noted. Scale rows between lowest rows of tubercles at midbody 36–40. Rows of dorsal tubercles at midbody 20–25. Precloacal pores in males 16–29, in a continuous series. Pores present, but much smaller in the single adult females paratype (CAS 222413), a single poreless scale dividing the rightmost pore from a continuous series of 13;

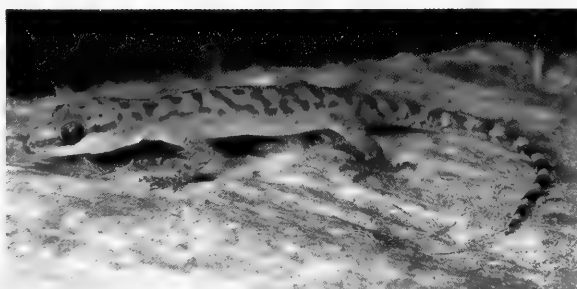


FIGURE 9. Living paratype specimen of *Cyrtodactylus gansi*, sp. nov. (CAS 222411) illustrating the dorsal coloration of the species. Photo by Hla Tun.

TABLE 3. Mensural data for the types of *Cyrtodactylus gansi*, sp. nov.  
Abbreviations as in Materials and Methods section; all measurements in mm.

	CAS 222414 <i>Holotype</i>	CAS 222411 <i>Paratype</i>	CAS 222412 <i>Paratype</i>	CAS 222413 <i>Paratype</i>	CAS 226144 <i>Paratype</i>	CAS 226145 <i>Paratype</i>
<i>Sex</i>	male	male	male	female	male	juvenile
<i>SVL</i>	60.8	46.5	57.3	62.4	62.3	29.3
<i>ForeaL</i>	8.9	7	8	8.6	8.5	4.5
<i>CrusL</i>	10.3	7.8	9.5	11	10.5	5.3
<i>TailL (entire)</i>	75.6	53.9	6.4	72	54.2	30.4
<i>TailL (portion regenerated)</i>	28.6	—	broken	—	47.8	—
<i>TailW</i>	5.9	3.9	5.8	4.2	4.9	2.2
<i>TrunkL</i>	28.1	20.6	25.7	30.3	25.2	11.5
<i>HeadL</i>	17.1	12.2	15.5	16.6	17.3	8.7
<i>HeadW</i>	10	7.8	9.4	9.9	10.2	5.6
<i>HeadH</i>	6.8	5	5.8	6	6.6	3.8
<i>OrbD</i>	4	2.7	3.9	4	4.3	2.1
<i>EyeEar</i>	4.2	3.9	4.5	4.6	5	2.6
<i>SnEye</i>	6.1	4.9	5.8	6.6	6.4	3.4
<i>NarEye</i>	4.5	3.1	3.8	4	4.6	2.3
<i>Interorb</i>	5.6	3.4	5	5.7	5.5	3.3
<i>EarL</i>	1.2	1.1	1.3	1.4	1.4	0.6
<i>Internar</i>	2.2	1.6	1.7	2.1	2	1.1

no precloacal groove in female specimen, no pores or groove in juvenile (CAS 226145). Supralabials to midpoint of orbit 7 on right side of CAS 222412 and 226144); infralabials 9 (CAS 226144, right) or 10 (CAS 222412 and CAS 226144, left). Supranasal scales in contact anteriorly in CAS 222413, one posterior internasal only in CAS 226144, two posterior internasals arranged longitudinally in CAS 222411.

Color pattern less fragmented on nape and shoulders in some specimens (CAS 222412, 226144), yielding 10 transverse bands to sacrum. Dorsal markings less bold and continuous in juvenile (CAS 226145). Thirteen (CAS 222411) or 15 (CAS 222413) dark tail bands in specimens with original tails.

**DIAGNOSIS.**— *Cyrtodactylus gansi* may be distinguished from all congeners on the basis of its possession of short digits, a single, strongly angled and somewhat recessed series of precloacal pores (16–29) in males (pores smaller and not in groove in females), absence of femoral pores, 20–25 longitudinal rows of dorsal tubercles; 36–40 ventral scales between lowest rows of dorsal tubercles (no discrete ventrolateral folds), subcaudal scalation without enlarged midventral plates, and dorsal pattern of approximately 10 narrow, dark transverse bands from occiput to sacrum, sometimes fragmented anteriorly.

Among other species from Myanmar it is most similar to *C. khasiensis* and *C. ayeyarwadyensis* (see account of latter species above), from which it may be distinguished by its shallow precloacal groove (in males) and its dorsal color pattern.

**DISTRIBUTION.**— *Cyrtodactylus gansi* is currently known only from high elevation (750–1300

m) at the type locality of Che Stream, Min Dat Township, Min Dat District in Chin State, in the southern Chin Hills (Fig. 3). The recently described *C. slowinskii*, previously known only from Alaungdaw Kathapa National Park, in the Sagaing Division, is the only congener thus far found at this locality (CAS 222415).

***Cyrtodactylus wakeorum* Bauer, sp. nov.**

Figs. 10–11

**HOLOTYPE.**— California Academy of Sciences (CAS) 221935 (Field number JBS 8948), adult female; Rakhine Yoma Elephant Range, Gwa, Gwa Township, Rakhine State, Myanmar ( $17^{\circ}35'02.4''\text{N}$ ,  $94^{\circ}40'44.2''\text{E}$ ); collected by Htun Win, Thin Thin, Kyi Soe Lwin and Awan Khwi Shein, 2 June 2001.

**PARATYPE.**— CAS 226148 (Field number JBS 8408), juvenile; Ye Bya Stream, Rakhine Yoma Elephant Range, Gwa Township, Rakhine State, Myanmar ( $17^{\circ}41'17.5''\text{N}$ ,  $94^{\circ}38'50.8''\text{E}$ , 180 m.); collected by J. B. Slowinski, G.O.U. Wogan, Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 25 April 2001.

**ETYMOLOGY.**— The specific epithet honors Marvalee H. Wake (born 1939) and David B. Wake (born 1936) of the University of California, Berkeley for their contributions to herpetology, vertebrate morphology and evolutionary biology and for their valuable mentoring of many graduate students, myself included. It gives me particular pleasure to name and describe this species on the occasion of the nominal retirement of my former dissertation advisor and mentor, Marvalee Wake. The specific epithet is masculine (mixed gender) and is formed in the genitive plural.

**DEFINITION.**— A small sized *Cyrtodactylus*, snout-vent length to 64 mm; body moderately slender, limbs and digits relatively short; one pair of enlarged postmental scales in broad contact behind mental; dorsum with relatively smooth texture, with 24 longitudinal rows of small, oval to rounded, keeled tubercles; 31 ventral scales across midbody; no precloacal groove, 12 precloacal pores in a single series in female holotype, no femoral pores. Ten subdigital lamellae beneath 4<sup>th</sup> toe of pes distal to basal digital inflection, six broad lamellae basal to inflection. Subcaudal scales not forming broad transverse plates. Dorsal pattern of 6 thin dark bands (one nuchal and five between shoulders and sacrum), each bordered posteriorly by a thin white line. Head without dorsal pattern. Tail with alternating light and dark banding.

**DESCRIPTION** (based on holotype, CAS 221935).— Adult female containing two eggs. Snout-vent length 63.8 mm. Head relatively short (HeadL/SVL ratio 0.25), moderately narrow (HeadW/HeadL ratio 0.59), not depressed (HeadH/HL ratio 0.43), distinct from neck.

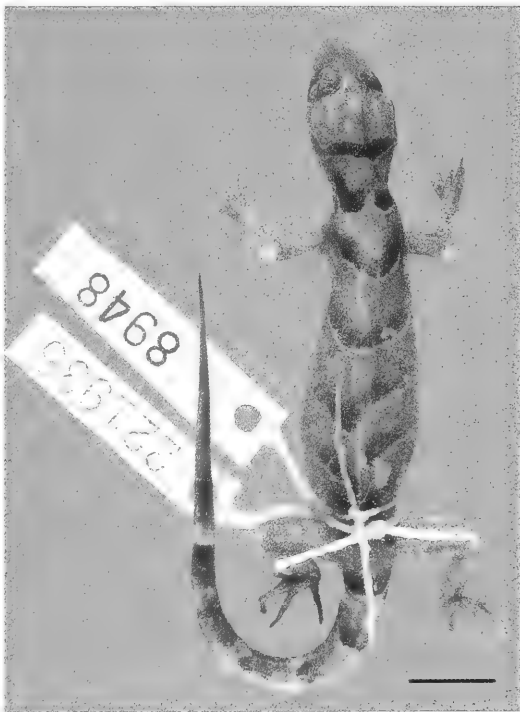


FIGURE 10. Holotype of *Cyrtodactylus wakeorum*, sp. nov. (CAS 221935) from Rakhine Yoma Elephant Range, Rakhine State, Myanmar. Note the relatively short digits, light-edged dark crossbands, and patternless head dorsum of this gravid female. Scale bar = 10 mm.

Lores and interorbital region weakly inflated, canthus rostralis not particularly prominent. Snout relatively short (SnEye/HeadL ratio 0.39); longer than eye diameter (OrbD/SnEye ratio 0.60); scales on snout and forehead rounded, granular, flattened to slightly conical, becoming heterogeneous posterior to mid-frontal region; scales on snout larger than those on occipital region. Eye relatively large (OrbD/HeadL ratio 0.25); pupil vertical with crenelated margins; supraciliaries short, without projecting spines. Ear opening oval, small (EarL/HeadL ratio 0.08); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.38). Rostral 64% as deep (1.6 mm) as wide (2.5 mm), incompletely divided dorsally by well developed rostral groove; two enlarged supranasals separated by a much smaller anterior internasal and two even smaller posterior internasals; rostral in contact with supralabial I, supranasals, and anterior internasal; nostrils circular, each surrounded by supranasal, rostral, first supralabial, one postnasal, and crescentic nasal, rostral contact of narial border extensive; narial flap partially occludes posterior half of nostril; 1–3 rows of scales separate orbit from supralabials. Mental subtriangular, wider (2.1 mm) than deep (1.6 mm); one pair of enlarged postmentals, each 50% size of mental, in broad contact with one another medially, bordered anterolaterally by first infralabial (and second infralabial on left side only), posterolaterally by enlarged lateral chinshield, and posteriorly by 3 chin granules. Infralabials bordered medially by 1–2 rows of enlarged scales. Supralabials (to midorbital position) 8 (left) –9 (right); enlarged supralabials to angle of jaws 11; infralabials 10; interorbital scale rows across narrowest point of frontal 12.

Body relatively slender, relatively short (TrunkL/SVL ratio 0.40) with ventrolateral folds indistinct. Dorsal scales small, granular, conical, with regularly arranged small tubercles extending from frontal region on to tail base; each tubercle oval to rounded, bearing a single prominent keel; tubercles becoming smaller and less prominently keeled on flanks; largest keeled tubercles in approximately 24 regular rows at midbody. Ventral scales larger than dorsal, smooth, subimbricate laterally, imbricate across midventer; somewhat larger than elsewhere along ventral midline of abdomen, and especially in precloacal region; midbody scale rows across belly to edge of flanks (as demarcated by dorsal color pattern) 31; gular region with homogeneous scalation. Precloacal pores in a single continuous series of 12; bordered posteriorly by a row of greatly enlarged poreless scales. No femoral pores or precloacal groove. Scales on palm and sole smooth, rounded; scales on dorsal aspects of forelimbs smooth, subimbricating, heterogeneous but without tubercles. Hindlimbs with small scattered tubercles.

Fore and hindlimbs relatively stout; forearm short (ForeaL/SVL ratio 0.13); tibia short (CrusL/SVL ratio 0.16); digits moderately short, strongly inflected at basal interphalangeal joints, all bearing robust, slightly recurved claws; subdigital lamellae rounded, smooth, without scansorial surfaces; lamellae distal to much enlarged scale at basal digital inflection and not including ventral claw sheath: 4–4–5–5–5 (manus), 3–4–5–6–5 (pes), proximal 1–3 fragmented on most digits; enlarged basal lamellae ( $\geq$  twice size of palmar scales) to and including enlarged scale at basal inflection: 6–7–9–9–8 (manus), 7–7–10–10–11 (pes); interdigital webbing absent. Relative length of digits (manus; measurements in mm in parentheses): III (4.3) > IV (4.0) > II (3.4)  $\approx$  V (3.3) > I (2.2); (pes): IV (5.9) > III (5.2)  $\approx$  V (5.1) > II (3.9) > I (2.9).

Tail partly regenerated, slightly longer than body (TailL/SVL ratio 1.08), slender, tapering; divided into indistinct segments, each 8–9 dorsal scale rows in length; two rows of enlarged, flattened, keeled tubercles positioned paravertebrally on tail base only, remaining dorsal caudal scales small, smooth, rectangular; subcaudal scales larger (3 per tail segment), smooth, imbricate not forming a single series of transverse plates. Two enlarged, smooth, conical postcloacal spurs on each side of tailbase.

Osteology. Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for

manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 17.5 post pygal caudal vertebrae in original tail in holotype (25 post pygal vertebrae in original tail of juvenile paratype). Adult female holotype containing two large eggs. No cloacal bones present in female, not discernable in juvenile. Juvenile paratype with most bones incompletely ossified. Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative). Base color mid brown. Boldly marked with a series of chocolate brown bands, each outlined posteriorly by a thin cream to whitish border one scale width in thickness. Occipital band turns at a right angle above and behind ear and extends anteriorly to orbit and under eye to loreal region, portion on temporal region almost completely surrounded by thin white border. Dorsum of head unpatterned. Nuchal markings paired, borders just touching one another along midline. Five additional bands between shoulders and sacrum, each successively more chevron-shaped, becoming more asymmetrical posteriorly. Dark markings faded on flanks. Limbs more-or-less uniform mid-brown with scattered small whitish markings. Hindlimb insertions with a large chocolate brown blotch at anterior border. Venter beige tinged by the light brown speckling of individual scales, except along midline. Tail with alternating chocolate brown and mid brown to cream banding. Paler bands wider than darker basally. Tail venter with scattered dark pigmentation, especially distally. Dorsal caudal color pattern extends onto ventrum, especially posteriorly.

Base color in life pinkish brown, venter whitish. Light borders around dark dorsal markings, and supraciliary scales yellowish to yellowish-orange. Iris golden brown (Fig. 11).

**VARIATION.**—Comparative mensural data for the holotype and paratype are presented in Table 4. The juvenile paratype (CAS 226148) is similar to the holotype in most respects except: left postmental scale fragmented into two scales; nostril bordered posteriorly by three postnasals; enlarged supralabial scales to middle of eye 9 (left) and 10 (right), to corner of mouth 11 (left) and 12 (right), infralabials 9 (left) and 10 (right); precloacal pores not developed, tail tip broken, occipital band not connected to temporal markings, nape markings fused to form a single band, more posterior bands paired, dark blotches at posterior border of hindlimb insertions. Both the holotype and paratype exhibit some skin abrasions, suggesting that the skin in life may be relatively delicate.

**DIAGNOSIS.**—*Cyrtodactylus wakeorum* may be distinguished from all congeners on the basis of its possession of relatively short limbs and digits, one pair of enlarged postmental scales in broad contact behind mental; dorsum with relatively smooth texture, with 24 longitudinal rows of tubercles, 31 ventral scales across midbody, ventrolateral folds absent, no precloacal groove, 12 precloacal pores in a single series in female holotype, no femoral pores, subcaudal scales not forming broad transverse plates, dorsal pattern of 6 thin dark bands (one nuchal and five between shoulders and sacrum), each bordered posteriorly by a thin white line, and head without dorsal pattern.

*Cyrtodactylus wakeorum* is superficially most similar to *C. consobrinoides* and, to a lesser extent, *C. annandalei*. It may be distinguished from the former by its possession of lack of subcaudal transverse plates, and its patternless head dorsum. It differs from the latter in its greater number of dorsal tubercle rows (24 vs 16–18), smaller number of ventral scale rows (31 vs 43), and light borders around only the posterior margins of the dark dorsal markings. Unfortunately the absence of adult male specimens precludes the use of certain precloacal and femoral pore charac-



FIGURE 11. Living holotype of *Cyrtodactylus wakeorum*, sp. nov. (CAS 221935) illustrating the yellowish edging of the dorsal bands and the supraciliary scales. Photo by Hla Tun.

ters which might further distinguish *C. wakeorum* from its congeners. Comparisons with other species are provided following the description of all new taxa.

**DISTRIBUTION.**—*Cyrtodactylus wakeorum* is known only from Rakhine Yoma Elephant Range, southern Rakhine State (Fig. 3). It is there sympatric with *C. ayeyarwadyensis*.

***Cyrtodactylus russelli* Bauer, sp. nov.**

Figs. 12–14

**HOLOTYPE.**—California Academy of Sciences (CAS) 226137 (Field number JBS 15525), adult male; upper Nat E-Su Stream, Htamanthi Wildlife Sanctuary, Hkamti Township, Sagaing Division, Myanmar (25°28'27.7"N, 95°37'20.5"E, 227 m.); collected by Htun Win, Thin Thin and Awan Khwi Shein, 8 November 2002.

**PARATYPE.**—CAS 226140 (Field number JBS 18088), adult female; Hepu Stream, Indawgyi Wildlife Sanctuary, Mohuyin Township, Kachin State, Myanmar (25°05'38.2"N, 96°22'49.0"E); collected by J.A. Wilkinson, G.O.U. Wogan, J.V. Vindum, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 16 May 2003.

**ETYMOLOGY.**—The specific epithet honors my friend and colleague Anthony P. Russell (born 1947) of the University of Calgary for his many contributions to the study of gekkonid lizards and for his influence on my professional career. The epithet is masculine and is formed in the genitive singular.

**DEFINITION.**—A large sized *Cyrtodactylus*, snout-vent length to 116 mm; body moderately slender, elongate with well developed ventrolateral folds, limbs stout, digits long; one pair of enlarged postmental scales in broad contact behind mental; dorsum with 22 longitudinal rows of small, conical to keeled tubercles; 35–41 ventral scales across midbody to ventrolateral folds; no precloacal groove, 15 precloacal pores in a single series in male holotype, 16–19 femoral pores on each thigh separated from precloacal pores by a diastema (precloacal and femoral pores absent in female paratype). Thirteen subdigital lamellae beneath 4<sup>th</sup> toe of pes distal to basal digital inflection, nine broad lamellae basal to inflection. Subcaudal scales forming broad transverse plates, but distinctly narrower than tail. Dorsal pattern poorly defined, including dark elongate blotches or bands and scattered lighter blotches on flanks. Tail with alternating light and dark banding.

**DESCRIPTION** (based on holotype, CAS 226137, except as noted).—Adult male with abdominal incision from tissue removal. Snout-vent length 105.7 mm. Head relatively long (HeadL/SVL ratio 0.28), wide (HeadW/HeadL ratio 0.64), not depressed (HeadH/HL ratio 0.41), distinct from neck. Lores and interorbital



FIGURE 12. Holotype of *Cyrtodactylus russelli*, sp. nov. (CAS 226137) from Htamanthi Wildlife Sanctuary, Sagaing Division, Myanmar. Note the long digits, robust body, and obscure dorsal pattern. Scale bar = 10 mm.



region strongly inflated, canthus rostralis well developed. Snout moderately short (SnEye/HeadL ratio 0.39); longer than eye diameter (OrbD/SnEye ratio 0.60); scales on snout and forehead rounded, granular to weakly conical, intermixed with scattered small tubercles posterior to fronto-parietal suture; scales on snout much larger than those on occipital region. Eye relatively small (OrbD/HeadL ratio 0.23); pupil vertical with crenelated margins; supraciliaries short, each posterior or supraciliary bearing a short spines Ear opening rounded, partly occluded by horizontal fold of skin, small (EarL/HeadL ratio 0.04); eye to ear distance greater than diameter of eyes (EyeEar/OrbD ratio 1.17). Rostral 64% as deep (2.6 mm) as wide (4.1 mm), divided dorsally by a weakly developed inverted "V"-shaped rostral groove extending about 20% of scale height; two enlarged supranasals separated by two somewhat smaller and irregular internasals; rostral in contact with supralabial I, supranasals, and two internasals; nostrils oval, laterally oriented, each surrounded by one supranasal, rostral, first supralabial, one postnasal, and a larger crescentic nasal, rostral contact of narial border extensive; narial flap partially occludes posterior 2/3 of nostril; 3–5 rows of scales separate orbit from supralabials. Mental subtriangular, much wider (3.7 mm) than deep (3.1 mm); one pair of enlarged postmentals, each approximately 40% size of mental, in broad contact with one another medially, bordered anterolaterally by first infralabial, posterolaterally by enlarged lateral chinshield, and posteriorly by 4 small chin granules. Infralabials bordered medially by 2–3 rows of enlarged scales. Supralabials (to midorbital position) 9; enlarged supralabials to angle of jaws 11 (left) to 12 (right); infralabials 10 (left) to 11 (right); interorbital scale rows across narrowest point of frontal 28.

Body relatively robust, elongate (TrunkL/SVL ratio 0.47) with weakly denticulate, well developed ventrolateral folds. Dorsal scales heterogeneous, rounded, granular to weakly conical, intermixed with regularly arranged small (6–8 times granule size), keeled, rounded tubercles extending from parietal region on to back and tail base; tubercles on nape more strongly conical and without keels; tubercles in approximately 22 longitudinal rows at midbody; 42 tubercles in paravertebral row from occiput to mid sacrum. Ventral scales much larger than dorsal, cycloid, smooth, subimbricate to imbricate; not enlarged under thighs or between precloacal pores and vent; midbody scale rows across belly between ventrolateral folds 35; scales on throat minute, granular, grading into larger scales on chest. Precloacal pores in a single continuous series of 15, in a weakly developed groove; 19 femoral pores on left thigh, 16 on right thigh, each series separated from precloacal pore series by 3 poreless scales; Scales on palm and sole smooth, flattened; scales on dorsal aspects of limbs granular to conical, similar to dorsal scales, with larger, conical tubercles interspersed.

Fore and hindlimbs relatively short, stout; forearm short (ForeaL/SVL ratio 0.15); tibia short (CrusL/SVL ratio 0.17); digits long, strongly inflected at basal interphalangeal joints, all bearing robust, slightly recurved claws; subdigital lamellae rounded, smooth, without scansorial surfaces, widened beneath basal phalanx to almost width of toes; lamellae from first proximal scansor greater than twice largest plam scale to basal digital inflection: 5–7–7–7–8 (manus), 6–8–8–9–8 (pes); lamellae from basal inflection to toe tip, not including ventral claw sheath: 10–10–13–10–11 (manus), 9–11–13–13–13 (pes); one to several rows of distal lamellae fragmented; interdigital webbing present, especially between digits II and III and III and IV, but weakly developed. Relative length of digits (manus; measurements in mm in parentheses): IV (10.4) > V (10.0) > III (9.3) > II (8.2) > I (6.0); (pes): V (11.6)  $\simeq$  IV (11.5) > III (10.9) > II (9.0) > I (6.0).

Tail in holotype broken at base. Original tail in paratype longer than body (TailL/SVL ratio 1.19), slender, tapering, slightly depressed in corss section. Scales arranged in regular whorls; ventral scales rectangular, dorsal scales rounded at free margins or hexagonal. 9 circumferential rows of dorsal scales per tail segment; basalmost postpygal segment with one transverse row of 10 enlarged keeled tubercles, each tubercle separated from the next by 1–4 smaller scales; more dis-

tally tubercles decreasing by pairs to just two per transverse row; posteriormost caudal scales narrow and relatively elongate. Subcaudal scales much larger, 2 per tail segment, each transversely enlarged but distinctly narrower than tail; tail segmentation weakly demarcated ventrally. Cloacal spurs with 3–4 slightly enlarged, smooth, rounded scales on each side of tailbase.

**Osteology.** Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 1.5 post pygal caudal vertebrae in regenerated tail in holotype (39 post pygal vertebrae in original tail of paratype). One pair of crescentic cloacal bones present, expanded posterolaterally (absent in female paratype). Endolymphatic sacs not enlarged extracranially.

**Coloration** (in preservative). Dorsum mid- to dark brown with poorly differentiated darker markings forming elongate paravertebral blotches and more-or-less continuous longitudinal bands of variable thickness on the dorsolateral margins of trunk (Fig. 12); lighter longitudinally oriented blotches on flanks. A series of three grayish spots with irregular margins across shoulders. Forelimb insertions and axillae pale grayish. Forelimbs mottled brown, hindlimbs mottled brown but with some irregular grayish barring proximally; head darker than trunk, without obvious markings; loreals and area beneath orbit somewhat darker than rest of head; labial pale with scattered dark pigment on all scales. Venter grayish cream with dark pigment on limb margins and on throat and margins of jaws; scattered pigment across all ventral scales. Tail dorsum with alternating wider darker bands and narrower light brown bands; 9 dark bands on original tail; caudal color pattern extends onto venter, more distinct posteriorly (based on paratype).

Pattern much bolder in life, consisting of a series of wavy-edged, transverse dark markings with thin, pale borders. Anteriormost marking continuous across occiput, nape and shoulder markings fragmented, four continuous markings across body and sacrum (Fig. 13). Large brown patch continuous from snout to anterior of forelimb insertion (Fig. 14). Iris bronze.

**VARIATION.**— Comparative mensural data for the holotype and paratype are presented in Table 4. Adult female paratype (CAS 226140) differs from holotype in: internasals 2 but arranged along body axis, not transversely; rostral crease straight, not “V”-shaped; 9 (right) to 10 (left) supralabials to middle of eye, 11 (right) to 12 (left) to corner of mouth, 9 (right) to 10 (left) infralabials; 41 ventral scales between ventrolateral folds; 44 tubercles in paravertebral row from occiput

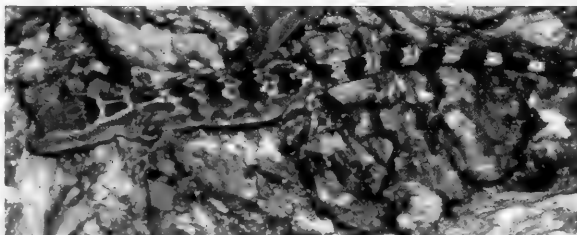


FIGURE 13. Living paratype of *Cyrtodactylus russelli*, sp. nov. (CAS 226140) illustrating the dorsal pattern of wavy dark cross-bars. Photo by Hla Tun.

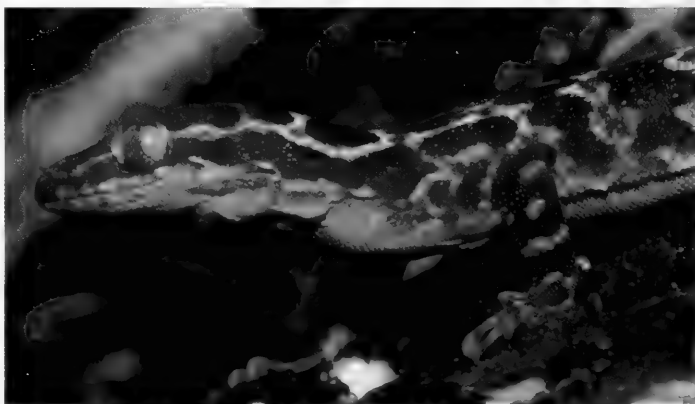


FIGURE 14. Lateral view of living paratype of *Cyrtodactylus russelli*, sp. nov. (CAS 226140) illustrating the large brown patch on the side of head and neck, whitish outline of dorsal markings, beige venter, and golden iris. Photo by Hla Tun.

TABLE 4. Mensural data for the types of four new species of *Cyrtodactylus*. Abbreviations as in Materials and Methods section; all measurements in mm.

	<i>C. wakeorum</i>		<i>C. russelli</i>		<i>C. chrysopylos</i>	<i>C. aequalis</i>
	CAS 221935 <i>Holotype</i>	CAS 226148 <i>Paratype</i>	CAS 226137 <i>Holotype</i>	CAS 226140 <i>Paratype</i>	CAS 226141 <i>Holotype</i>	CAS 222185 <i>Holotype</i>
<i>Sex</i>	female	? (juvenile)	male	female	female	female
<i>SVL</i>	63.8	33	105.7	116	79.1	90.1
<i>ForeaL</i>	8.5	4.9	16	17.9	13.2	14
<i>CrusL</i>	10	5.6	18.3	20.5	16.1	16.2
<i>TailL (entire)</i>	69	31.8	11	138.6	6.2	92.1
<i>TailL (portion regenerated)</i>	24	bBroken	broken	—	broken	49.5
<i>TailW</i>	5.1	2.4	10.6	10.6	7	7
<i>TrunkL</i>	28.4	14.1	49.4	52.3	36	38.8
<i>HeadL</i>	15.9	10.2	29.2	31.4	22.4	24.3
<i>HeadW</i>	9.4	5.5	18.6	22.2	14	15.9
<i>HeadH</i>	6.9	3.7	11.8	12.9	9.3	10.1
<i>OrbD</i>	4	2.7	6.8	7.4	6.3	6.6
<i>EyeEar</i>	5.4	2.7	8	9.3	5.5	6.5
<i>SnEye</i>	6.4	4.1	11.2	12.2	9.4	9.8
<i>NarEye</i>	4.8	2.8	8.2	8.9	6.6	7.3
<i>Interorb</i>	5.9	3.5	10.6	11.7	8.3	8.3
<i>EarL</i>	1.2	0.8	1	1.6	2.1	2
<i>Internar</i>	1.6	1.1	3.8	3.6	2.6	3.2

to mid-sacrum; no precloacal or femoral pores; tail original; dorsal markings more pronounced than in holotype, consisting of dark brown and grayish mottling; dark paravertebral markings on nape prominent; dark occipital band present; a narrow whitish line across occiput, fading on temporal region.

**DIAGNOSIS.**— *Cyrtodactylus russelli* may be distinguished from all congeners on the basis of its very large size (to 116 mm SVL), ventrolateral folds well developed, digits long, dorsum with 22 longitudinal rows of tubercles, 35–41 ventral scales across midbody to ventrolateral folds, no precloacal groove, 15 precloacal pores in a single series in male holotype, 16–19 femoral pores on each thigh separated from precloacal pores by a diastema (precloacal and femoral pores absent in female paratype), subcaudal scales forming broad transverse plates, but distinctly narrower than tail width, and dorsal pattern poorly defined, including dark elongate blotches or bands and scattered lighter blotches on flanks.

Among its congeners in Myanmar, the new species is approached in size only by *C. slowinskii* (maximum SVL 108 mm), to which it appears closely related. It differs from this species in its less well demarcated dorsal pattern, white (vs yellowish) light markings, predominantly transverse wavy dorsal markings (vs paired blotches), and larger number of precloacal pores (15 vs 9–11) and femoral pores (16–19 per thigh vs 11–12). Comparisons with other species are provided following the new species descriptions.

**DISTRIBUTION.**— *Cyrtodactylus russelli* is known from two localities (Htamanthi Wildlife

Sanctuary, Sagaing Division and Indawgyi Wildlife Sanctuary, Kachin State), approximately 85 km apart in northern Myanmar. The region lies between the border ranges with Assam, India and the Mangin and Kumon Ranges in the east. It occurs with *C. khasiensis* at Htamanthi (CAS 226138). Given the limited sampling in this region of Myanmar, it is impossible to estimate the extent of the species' range as a whole. Although no similar geckos have been recorded from Assam, sampling in this region of India remains inadequate and it may yet be recorded outside of Myanmar.

***Cyrtodactylus chrysopylos* Bauer, sp. nov.**

Figs. 15–17

**HOLOTYPE.**—California Academy of Sciences (CAS) 226141 (Field number JBS 13417), adult male; Panlaung-Pyadalin Cave Wildlife Sanctuary, Ywa Ngan Township, Shan State, Myanmar (21°07'58.4"N, 96°20'25.0"E, 319 m.); collected by G.O.U. Wogan, R.S. Lucas, J.V. Vindum, Htun Win, Thin Thin, Awan Khwi Shein and H. Tun, 14 July 2002.

**ETYMOLOGY.**—The specific epithet is derived from the Greek *chrysos* (golden) and *pylos* (gate) and refers to Golden Gate Park, San Francisco the location of the California Academy of Sciences, which spearheaded the herpetological surveys of Myanmar that revealed this and many other new taxa. The name commemorates the 150<sup>th</sup> anniversary of the Academy and its long history of herpetological research in Asia. I particularly express my gratitude to the curators and curatorial staff of the Department of Herpetology for their support of my research and field expeditions over the past 20 years. The epithet is a masculine noun in apposition.

**DEFINITION.**—A moderately sized *Cyrtodactylus*, snout-vent length of unique holotype 79 mm; body slender, elongate, limbs and digits long; one pair of enlarged post-mental scales in broad contact behind mental; dorsum with 16 longitudinal rows of small, keeled tubercles; 37 ventral scales across midbody to distinct ventrolateral folds; no precloacal groove or femoral pores, 10 precloacal pores in a single series; a single, much larger, pored scale posterior to precloacal series and separated from it by a single, enlarged scale without pores. Thirteen subdigital lamellae beneath 4<sup>th</sup> toe of pes distal to basal digital inflection, six broad lamellae basal to inflection. Dorsal pattern of distinct alternating brown and white bands (one on occiput, one across shoulders, six between limb insertions, one on sacrum, two on pygal portion of tail).

**DESCRIPTION** (based on holotype, CAS 226141).—Adult female with midventral incision from tissue removal. Snout-vent length 79.1 mm. Head relatively long (HeadL/SVL ratio 0.28), moderately wide (HeadW/HeadL ratio 0.62), not depressed (HeadH/HL ratio 0.42), distinct from neck. Lores and interorbital region inflated, canthus rostralis not particularly prominent. Snout moderately long (SnEye/HeadL ratio 0.42); much longer than eye diameter (OrbD/SnEye ratio 0.67); scales on snout and forehead



FIGURE 15. Holotype of *Cyrtodactylus chrysopylos*, sp. nov. (CAS 226141) from Panlaung-Pyadalin Cave Wildlife Sanctuary, Shan State, Myanmar. Note the long digits, slender limbs, and alternating light and dark dorsal markings. Scale bar = 10 mm.

rounded, granular, flattened to slightly conical, becoming heterogeneous posterior to frontal region; scales on snout larger than those on occipital region. Eye large (OrbD/HeadL ratio 0.28); pupil vertical with crenelated margins; supraciliaries short, with small, blunt spines. Ear opening oval, large (EarL/HeadL ratio 0.09); eye to ear distance less than diameter of eyes (EyeEar/OrbD ratio 0.88). Rostral 56% as deep (1.9 mm) as wide (3.4 mm), dorsal half incompletely divided by rostral groove; two enlarged supranasals separated by a single, smaller internasals; rostral in contact with supralabial I, supranasals, and internasal; nostrils circular, each surrounded by supranasal, rostral, first supralabial, and two postnasals, rostral and supralabial contact of narial border extensive; narial flap partially occludes posterior third of nostril; 2–4 rows of scales separate orbit from supralabials. Mental subtriangular, much wider (3.6 mm) than deep (2.8 mm); one pair of enlarged postmentals, each 30% size of mental, in broad contact with one another medially, bordered anterolaterally by first infralabial, posterolaterally by enlarged lateral chinshield, and posteriorly by 3 chin granules. Infralabials bordered medially by 1–3 rows of enlarged scales, largest anterior and lateral. Supralabials (to midorbital position) 8 (left) –9 (right); enlarged supralabials to angle of jaws 11; infralabials 10; interorbital scale rows across narrowest point of frontal 19.

Body relatively slender, elongate (TrunkL/SVL ratio 0.45); ventrolateral folds small but distinct, without denticulate margins. Dorsal scales small, granular to weakly conical, with regularly arranged small tubercles extending from frontal and temporal regions on to tail base; each tubercle rounded, bearing a single prominent keel; tubercles becoming smaller and less prominently keeled on flanks; largest keeled tubercles in approximately 16 regular rows at midbody. Ventral scales much larger than dorsal, smooth, subimbricate on abdomen, imbricate across chest; somewhat larger than elsewhere along ventral midline of chest and abdomen, and especially in precloacal region; midbody scale rows across belly between ventrolateral folds 37; gular region with homogeneous scalation. Precloacal pores in a single continuous series of 10 enlarged scales, bordered posteriorly by an enlarged poreless median scale, this in turn bordered posteriorly by an even larger pored scale (Fig. 16). No femoral pores or precloacal groove. Scales on palm and sole smooth, rounded; scales on dorsal aspects of proximal forelimbs smooth to weakly conical, relatively homogeneous. Hindlimbs and distal forelimbs with scattered conical tubercles.

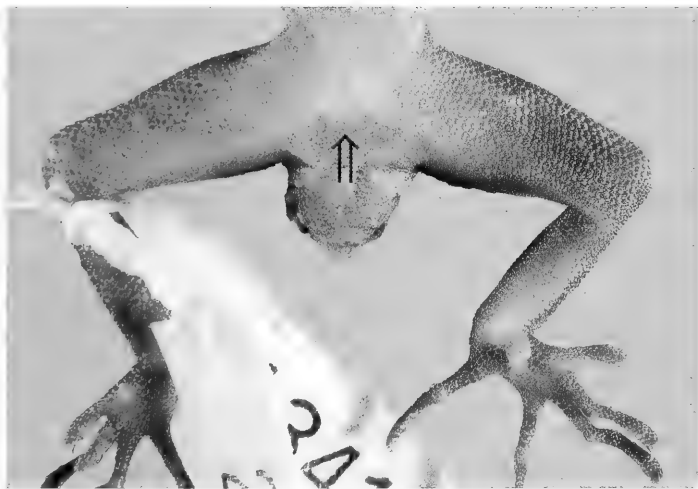


FIGURE 16. Cloacal region of *Cyrtodactylus chrysopylos*, sp. nov. (CAS 226141) showing the precloacal pore-bearing scales, including the very large scale posterior to the main series (arrow). Note also the absence of enlarged femoral scales.

Fore- and hindlimbs long, stout; forearm long (ForeaL/SVL ratio 0.17); tibia long (CrusL/SVL ratio 0.20); digits relatively long, strongly inflected at basal interphalangeal joints, all bearing robust, slightly recurved claws; subdigital lamellae rounded, smooth, without scansorial surfaces, widened beneath basal phalanx to approximately  $\frac{3}{4}$  width of toes; lamellae from first proximal scansor greater than twice largest palmar scale to basal digital inflection: 3–6–5–6–5 (manus), 5–6–6–6–6 (pes); lamellae from basal inflection to toe tip, not including ventral claw sheath:

10–10–11–12–12 (manus), 11–12–13–13–14 (pes); one to several rows of distal lamellae fragmented; very weakly developed interdigital webbing present, especially between digits II and III and III and IV, but weakly developed. Relative length of digits (manus; measurements in mm in parentheses): IV (7.9) > III (7.2) > V (6.70) > II (6.2) > I (4.7); (pes): IV (9.3) > III (8.5) > V (8.2) > II (6.7) > I (4.4).

Tail broken at base; 3 enlarged, smooth, blunt, conical postcloacal spurs on each side of tail-base.

Mensural data are presented in Table 4.

Osteology. Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 0.5 post pygal caudal vertebrae in regenerated tail in unique holotype. No cloacal bones present in female type. Endolymphatic sacs not enlarged extracranially.

Coloration (in preservative). Base color a mottled mid brown. Strongly marked with alternating chocolate brown and white bands. Dark occipital band extending anteriorly to orbit and under eye to nostril, becoming less well defined anterior of orbit; bordered above by a broken white line extending to posterior supraciliaries, bordered posteriorly by a thick white line passing through ear and onto supralabials. Supraciliaries white, a diffuse white line from anterior of orbit to nostril. Additional pairs of light and dark alternating bands across shoulders, 6 such pairs between limb insertions and one across sacrum; 2 additional such pairs on pygal portion of tail. Pattern roughly bilaterally symmetrical, faded on lower flanks. Dorsum of head with 4 diffuse dark marks on parietal table, largest at posterior margin of orbit. Posterior supralabials white, anterior supralabials whitish scattered white spots. Forelimbs mottled, with white blotches on limbs and limb insertions; hindlimbs with ill-defined alternating dark brown and white markings. Hindlimb insertions with large chocolate brown blotches at posterior border of thighs. Venter beige tinged by the light brown speckling of individual scales, especially on the borders of the jaws.

Base color in life purplish brown. Larger light dorsal markings with a yellowish cast, smaller lateral spots whitish. Throat white with a pinkish suffusion. Venter beige to light brown (Fig. 17).

**DIAGNOSIS.**—*Cyrtodactylus chrysopylos* may be distinguished from its congeners by its relatively long digits, 16 longitudinal rows of dorsal tubercles; 37 ventral scales across midbody to distinct ventrolateral folds, 10 precloacal pores in a single series, a single, greatly enlarged pored scale posterior to apex of precloacal series (Fig. 16), and dorsal pattern of distinct alternating brown and white bands (one on occiput, one across shoulders, six between limb insertions, one on sacrum, two on pygal portion of tail).

As the species is known only from a single female, the reliability of precloacal and femoral pore characteristics may be called into question, as such features often differ between genders. However, female *Cyrtodactylus*, if different from males, typically have a reduced number of pores, or may lack femoral or both femoral and precloacal pores all together. In this instance the presence in a female of a distinctive large pored scale posterior to the precloacal series is very likely to be present in males as well. This feature is unique among *Cyrtodactylus* and is alone sufficient to diagnose *C. chrysopylos* from all of its con-

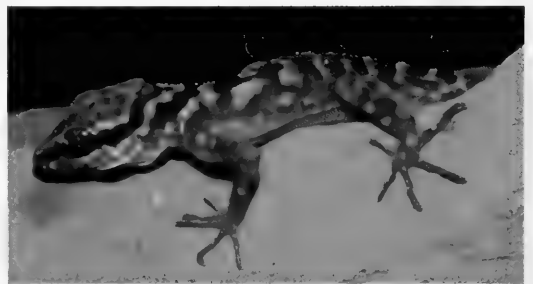


FIGURE 17. Living holotype of *Cyrtodactylus chrysopylos*, sp. nov. (CAS 226141) illustrating the yellowish and whitish dorsal and lateral markings and the long slender digits. Photo by Hla Tun.

genera. In addition, its distinctive dorsal pattern of nine bands between occiput and sacrum is unique.

**DISTRIBUTION.**— *Cyrtodactylus chrysopylos* is known only from Panlaung-Pyadalin Cave Wildlife Sanctuary in Shan State, Myanmar at an elevation of 319 m. This locality lies in the western portion of the extensive hill region occupying east central Myanmar. The new species is sympatric with *C. peguensis* at Panlaung-Pyadalin Wildlife Sanctuary (CAS 226142–226143).

***Cyrtodactylus aequalis* Bauer, sp. nov.**

Figs. 18–20

**HOLOTYPE.**— California Academy of Sciences (CAS) 222185 (Field number JBS 10347), adult male; Kyaik-Hti-Yo Wildlife Sanctuary, Kyaik Hto Township, Mon State, Myanmar (17°26'38.1"N, 97°05'56.8"E); collected by Htun Win, Thin Thin and Awan Kwi Shein, 21 November 2001.

**ETYMOLOGY.**— The epithet is derived from the Latin *aequalis* meaning “same,” in reference to the fact that the number of dorsal tubercle rows equals the number of ventral scale rows across midbody between the ventrolateral folds. This condition is unique among species of *Cyrtodactylus*. The epithet is an adjective in the nominative singular.

**DEFINITION.**— A moderately sized *Cyrtodactylus*, snout-vent length of unique holotype 90 mm; body slender, limbs robust, digits long; one pair of enlarged postmental scales in broad contact with one another behind mental; dorsum with 24 longitudinal rows of relatively large, strongly keeled tubercles; 24 enlarged ventral scales between distinct ventrolateral folds; no precloacal groove, 9 minute precloacal pores in female type, 3–4 minute femoral pores separated from precloacal pores by a diastema. Fourteen subdigital lamellae beneath 4<sup>th</sup> toe of pes distal to basal digital inflection, eight broad lamellae proximal to inflection. Subcaudal scales forming transverse plates approximately 2/3 width of tail. Dorsal pattern of paired dark markings bordered by thin white lines (one on occiput, one across shoulders, five between limb insertions). Top of head with white vermiform marks on parietal table and frontonasal region. Tail with alternating light and dark bands.

**DESCRIPTION** (based on holotype, CAS 222185).— Adult female. Snout-vent length 90.1 mm. Head relatively long (HeadL/SVL ratio 0.27), wide (HeadW/HeadL ratio 0.66), not depressed (HeadH/HL ratio 0.42), distinct from neck. Lores and interorbital region inflated, canthus rostralis not especially well developed. Snout moderately long (SnEye/HeadL ratio 0.41); much longer than eye diameter (OrbD/SnEye ratio 0.66); scales on snout and forehead rounded, granular to slightly conical, intermixed with scattered small tubercles posterior to border of orbit; scales on snout larger than those on occipital region. Eye relatively large (OrbD/HeadL ratio 0.27); pupil vertical with crenelat-



FIGURE 18. Holotype of *Cyrtodactylus aequalis*, sp. nov. (CAS 222185) from Kyaik-Hti-Yo Wildlife Sanctuary, Mon State, Myanmar. Note the long digits and bold dorsal and head markings. Scale bar = 10 mm.

ed margins; supraciliaries short, posterior scales bearing small spines. Ear opening oval, vertically oriented, relatively large (EarL/HeadL ratio 0.08); eye to ear distance similar to diameter of eyes (EyeEar/OrbD ratio 0.98). Rostral 56% as deep (1.9 mm) as wide (3.4 mm), no rostral groove; two enlarged supranasals in broad median contact, a roughlt pentagonal internasal positioned between rostral and supranasals; rostral in contact with supralabial I, supranasals, and internasal; nostrils oval, laterally oriented, each in broad contact with rostral and first supralabial, also contacted by supranasal and two postnasals; pigmented narial flap partially occludes posterior half of nostril; 3–4 rows of scales separate orbit from supralabials. Mental subtriangular, slightly wider (2.9 mm) than deep (2.8 mm); one pair of enlarged postmentals, each 60–70% size of mental, in broad contact with one another medially, bordered anterolaterally by first infralabial, posterolaterally by enlarged lateral chinshield, the pair bordered posteriorly by 8 chin scales including several enlarged lateral chin scales. Infralabials bordered medially by 2–3 rows of enlarged scales. Supralabials (to midorbital position) 7; enlarged supralabials to angle of jaws 9 (left) to 10 (right); infralabials 10 (left) to 11 (right); interorbital scale rows across narrowest point of frontal 19.

Body relatively robust, relatively elongate (TrunkL/SVL ratio 0.43) with very weakly denticulate ventrolateral folds. Dorsal scales heterogeneous, mostly rounded to weakly conical granules with pitted or rugose surfaces, intermixed with regularly arranged, moderately large (8–10 times granule size), strongly keeled to mucronate, rounded tubercles extending from posterior border of orbits and temporal region on to tail base; tubercles on nape, head, and lower flanks more strongly conical and without keels; tubercles in approximately 24 longitudinal rows at midbody (Fig. 19); 39 tubercles in paravertebral row from occiput to mid-sacrum. Ventral scales much larger than dorsal, smooth, imbricate, enlarged along midventral line and in precloacal region; midbody scale rows across belly to ventrolateral folds 24 (Fig. 20); scales on throat minute, granular, rapidly grading into much larger scales on chest. Minute precloacal pores in a single continuous series of 9; 3 minute femoral pores on left thigh separated from precloacal pores by diastema of 7 poreless scales; right thigh with 4 femoral pores (with one poreless scale between the two most distal pores); femoral pores pierced in row of enlarged femoral scales; no precloacal groove. Scales on palm and sole smooth, flattened; scales on dorsal aspects of hindlimbs and forearms granular to weakly conical, similar to dorsal scales, with larger keeled tubercles interspersed; dorsal scales of proximal forelimbs without tubercles.

Fore- and hindlimbs relatively stout; forearm moderate (ForeaL/SVL ratio 0.15); tibia relatively long (CrusL/SVL ratio 0.18); digits long, strongly inflected at basal interphalangeal joints, all bearing robust, slightly recurved claws; subdigital lamellae rounded, smooth, without scansorial surfaces, widened beneath basal phalanx to approximately  $\frac{3}{4}$  width of toes; lamellae from first proximal scansor greater than twice largest plam scale to basal digital inflection: 5–6–7–7–7 (manus), 6–8–8–8–8 (pes); lamellae from basal inflection to toe tip, not including ventral claw sheath: 10–11–13–13–12 (manus), 11–11–13–14–16 (pes); interdigital webbing present, especially between digits II and III and III and IV, but weakly developed. Relative length of digits (manus; measurements in mm in parentheses): III (8.8) > IV (8.4) > V (7.2) > II (7.0) > I (5.5); (pes): IV (11.0) > V (10.4) > III (9.9) > II (8.1) > I (5.8).

Tail partly regenerated, slightly longer than body (TailL/SVL ratio 1.02), slender, tapering, somewhat depressed in cross section. Scales arranged in regular whorls, 8 dorsal scale rows per tail segment; pygal segment with one transverse row of 10 enlarged keeled tubercles, each tubercle separated from next by 1–3 smaller scales; on posterior portion of tail enlarged tubercles reduced to 4 per transverse row, becoming flattened and eventually unkeeled; tubercles absent on regenerated portion of tail, regenerated dorsal caudal scales somewhat irregular in shape, narrow and elongate. Subcaudal scales larger, 2 rows per tail segment, segments not strongly demarcated ventral-



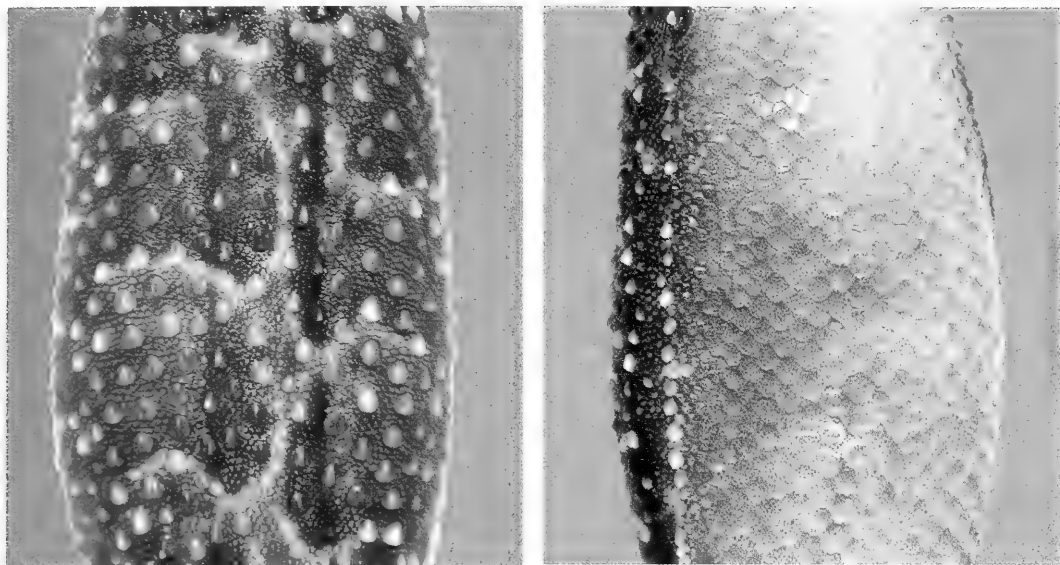


FIGURE 19 (left). Dorsum of holotype of *Cyrtodactylus aequalis*, sp. nov. (CAS 222185) illustrating the large, keeled tubercles of the dorsum (note: not all tubercle rows are visible in this view).

FIGURE 20 (right). Venter of holotype of *Cyrtodactylus aequalis*, sp. nov. (CAS 222185) illustrating the large, imbricate ventral scales and the well-demarcated ventrolateral margin.

ly; median subcaudal scales approximately 2/3 width of tail, forming a row of enlarged plates. Cloacal spurs with 3–4 enlarged, smooth, rounded scales on each side of tail base.

Mensural data are presented in Table 4.

**Osteology.** Parietal bones paired. Stapes imperforate. Phalangeal formulae 2–3–4–5–3 for manus and 2–3–4–5–4 for pes. Presacral vertebrae 26, including 3 anterior cervical (without ribs), 1 lumbar, and 2 sacral vertebrae; 5 pygal and 12.5 post pygal caudal vertebrae in regenerated tail of unique holotype. No cloacal bones present in female type. Endolymphatic sacs not enlarged extracranially.

**Coloration** (in preservative). Base color a medium brown with a series of pairs of dark brown markings bordered by thin (one scale row wide) white lines. Occipital band continuous with temporal stripe that continues to orbit and passes beneath eye. Ventral white line beneath dark temporal stripe continues onto supralabials and infralabials; dorsal white line above temporal stripe continues onto supraciliaries. A series of 5 partly coalescent blotches across nape, a pair of well demarcated blotches over shoulders, 5 pairs of increasingly asymmetrical marks between limb insertions, each with some degree of coalescence with its mate.

Top of head medium brown with a diffuse set of white vermiform marks on parietal table and frontonasal region. Canthal region crossed by a diffuse whitish stripe. A small white mark at anteroventral margin of orbit. Labials white with scattered brown blotches. Limbs barred with white bands extending onto digits, diffuse proximally, more well defined on forearm and crus. More clearly marked on hindlimb than forelimb. Tail with alternating light and wider dark brown bands. Asymmetrical distally, with white bands having dark brown centers. Regenerated portion of tail mottled mid-brown. Venter beige with much scattered brown pigment, especially on posterior abdomen, limb margins, throat and anterior chest. Underside of tail mottled dark brown with small white blotches.

**DIAGNOSIS.**— *Cyrtodactylus aequalis* may be distinguished from all congeners on the basis of

its long digits, dorsum with 24 longitudinal rows of relatively large, strongly keeled tubercles (Fig. 19), 24 enlarged ventral scales between distinct ventrolateral folds (Fig. 20), no precloacal groove, 9 minute precloacal pores in female type, 3–4 minute femoral pores separated from precloacal pores by a diastema, subcaudal scales forming transverse plates approximately 2/3 width of tail, dorsal pattern of paired dark markings bordered by thin white lines (one on occiput, one across shoulders, five between limb insertions), and top of head with white vermiform markings.

Although the comparison of the precloacal and femoral pore characters of the female type of *C. aequalis* with those of males has some limitations, it may be assumed that males also possess femoral pores, though the number of such pores may be higher. Pore characters aside, the relatively large number of dorsal tubercle rows and small number of ventral scale rows results in equal counts for these two parameters. This situation is unique in the genus and serves to diagnose the species from all other congeners. Comparisons with other species are presented below.

**DISTRIBUTION.**—*Cyrtodactylus aequalis* is known only from Kyaik-Hti-Yo Wildlife Sanctuary in Mon State in southern Myanmar, just to the west of the Gulf of Martaban (Gulf of Mottama).

### SPECIES COMPARISONS

The condition of precloacal and femoral scales and pores in males has traditionally been widely used to distinguish members of the genus *Cyrtodactylus* (e.g., Smith 1935; Darevsky and Szczerbak 1997; Bauer 2002). Unfortunately, three of the new species are represented only by adult females or juveniles. Nonetheless, two of these may be easily distinguished on the basis of unique features occurring in no other *Cyrtodactylus*: *C. chrysopylos* possesses a single, much larger, pored scale posterior to precloacal series and separated from it by a single, enlarged scale without pores (Fig. 13) and *C. aequalis* has greatly enlarged ventral scales (Fig. 17), resulting in an equal number of ventral midbody scale rows and longitudinal dorsal tubercle rows.

All of the remaining new species from Myanmar lack a deep precloacal groove (a shallow groove is present in male *C. gansi*) and can thus be distinguished from *C. annulatus* (Taylor, 1915), *C. cavernicolus* Inger and King, 1961, *C. fumosus* (Müller, 1895), *C. marmoratus* (Gray, 1831), *C. papuensis* (Brongersma, 1934), *C. philippinus* (Steindachner, 1867), *C. pubisulcus* Inger, 1958, *C. pulchellus* Gray, 1827, *C. rubidus* (Blyth, 1860), and *C. sadleiri* Wells and Wellington, 1984; they may be separated from *C. biordinis* Brown and McCoy, 1980 by the presence of a single vs. double row of femoral pores and from the following species by the presence of precloacal pores (at least in males): *C. jellesmae* (Boulenger, 1897), *C. laevigatus* Darevsky, 1964, *C. paradoxus* (Darevsky and Szczerbak, 1997), *C. sermowaiensis* (de Rooij, 1915), and most members of the subgenus *Geckoella* (*C. albofasciatus* [Boulenger, 1885], *C. collegalis* [Beddome, 1870], *C. deccanensis* [Günther, 1864], *C. jeyporensis* [Beddome, 1877], *C. nebulosus* [Beddome, 1870], and *C. yakhuna* [Deraniyagala, 1945]). All of the new species also lack the acutely angled, short precloacal pore series (maximum 12 pores) characteristic of *C. ingeri* Hikida, 1990 and *C. yoshii* Hikida, 1990, the denticulate tail margin of *C. brevipalmatus* (Smith, 1923), and the very short digits of *C. brevidactylus* Bauer, 2002 and *C. (G.) triedrus* (Günther, 1864).

*Cyrtodactylus annandalei* and *C. russelli* differ from the following species by the presence of femoral pores (at least in males): *C. adleri* Das, 1997, *C. angularis* (Smith, 1921), *C. ayeyarwadyensis* Bauer, 2003, *C. condorensis* (Smith, 1920), *C. consobrinoides* (Annandale, 1905), *C. elok* Dring, 1979, *C. fraenatus* (Günther, 1864), *C. gansi* Bauer, 2003, *C. intermedius* (Smith, 1917), *C. irianjayaensis* Rösler, 2001, *C. irregularis* (Smith, 1921), *C. khasiensis* (Jerdon, 1870), *C. lateralis* (Werner, 1896), *C. malayanus* (de Rooij, 1915), *C. matsuii* Hikida, 1990, *C. oldhami* (Theobald, 1876), *C. peguensis* (Boulenger, 1893), *C. quadrivirgatus* Taylor, 1962, *C. sumon-*

*thai* Bauer, Pauwels and Chanhom, 2002, and *C. sworderi* (Smith, 1925); and from the following species by the presence of a diastema between precloacal and femoral pore-bearing scales in males: *C. abrae* Wells, 2002; *C. feae* (Boulenger, 1893), *C. jarujini* Ulber, 1993, *C. loriae* (Boulenger, 1898), *C. lousiadensis* (de Vis, 1892), *C. malcolmsmithi* (Constable, 1949), *C. novaeguineae* (Schlegel, 1844), *C. papilionoides* Ulber and Grossmann, 1991, *C. tiomanensis* Das and Lim, 2000, *C. tuberculatus* (Lucas and Frost, 1900), *C. variegatus* (Blyth, 1859), and a new species from Saraburi Province, Thailand (Bauer et al., in press).

*Cyrtodactylus russelli* differs from the following species in having  $\leq 35$  ventral scale rows (vs  $\geq 40$ , except *C. darmandvillei*,  $\geq 36$ ): *C. annandalei*, Bauer, 2003, *C. baluensis* (Mocquard, 1890), *C. consobrinus* (Peters, 1871), *C. darmandvillei* (Weber, 1890), *C. derongo* Brown and Parker, 1973, *C. interdigitalis* Ulber, 1993, and *C. mimikanus* (Boulenger, 1914), and from the following in having 15 precloacal pores (vs.  $\leq 11$ ): *C. aaroni* Günther and Rösler, 2003, *C. agusanensis* (Taylor, 1915), *C. gubernatoris* (Annandale, 1913), *C. redimiculus* King, 1962, *C. slowinskii* Bauer, 2002, *C. wetariensis* (Dunn, 1927) and a new species from Kanchanaburi Province, Thailand (Bauer et al., in press). *Cyrtodactylus annandalei* differs from these same species (except *C. gubernatoris*) by its much smaller adult size (55 mm for an adult female vs. 70 mm and above). It differs from *C. gubernatoris* by its greater number of ventral scales across midbody (43 vs. 33).

*Cyrtodactylus ayeyarwadyensis*, *C. gansi* and *C. wakeorum* may be distinguished from the following species by their lack of transversely enlarged subcaudal plates: *C. abrae* Wells, 2002, *C. baluensis*, *C. condorensis*, *C. fraenatus*, *C. interdigitalis*, *C. intermedius*, *C. lousiadensis*, *C. sumonthai*, *C. tuberculatus*, *C. variegatus*, and a new species from Saraburi Province, Thailand (Bauer et al., in press); from the following by their smaller adult size ( $< 79$  mm SVL for *C. ayeyarwadyensis*,  $< 64$  mm for *C. wakeorum*, and  $< 63$  mm for *C. gansi* vs  $\geq 90$  mm SVL): *C. agusanensis*, *C. angularis*, *C. consobrinus*, *C. derongo*, *C. irianjayaensis*, *C. jarujini*, *C. loriae*, *C. matsuii*, *C. mimikanus*, *C. novaeguineae*, *C. papilionoides*, *C. russelli*, and *C. slowinskii*; from *C. adleri*, *C. elok*, *C. irregularis*, *C. oldhami*, *C. peguensis*, *C. quadrivirgatus*, and *C. sworderi* in having more than 8 precloacal pores; from *C. lateralis* and *C. malayanus* by their lower number of ventral scales ( $\leq 40$  vs  $\geq 50$ ); and from *C. malcolmsmithi* by their greater number of dorsal tubercle rows (20 or more vs 16).

*Cyrtodactylus ayeyarwadyensis* and *C. gansi* differ from the following species in having precloacal pores only (barely extending onto thighs in some *C. ayeyarwadyensis*): *C. aaroni*, *C. annandalei*, *C. darmandvillei*, *C. feae*, *C. gubernatoris*, *C. redimiculus*, *C. tiomanensis*, *C. wetariensis*, and a new species from Kanchanaburi Province, Thailand (Bauer et al., in press). Female *Cyrtodactylus wakeorum* may be similarly distinguished from these species, but the male condition is unknown. Regardless, *C. wakeorum* differs from all of these species in its particular dorsal pattern of dark, narrow crossbands edged posteriorly with yellow. *Cyrtodactylus ayeyarwadyensis* and *C. gansi* may be distinguished from *C. wakeorum* and *C. consobrinoides* by the absence of enlarged femoral scales. Differences among *C. khasiensis*, *C. ayeyarwadyensis*, and *C. gansi*, and between *C. wakeorum* and *C. consobrinoides*, respectively, are discussed in the diagnostic sections of the new species accounts above.

## DISCUSSION

Herpetofaunal diversity of Myanmar has long been underestimated, chiefly owing to limited collecting activity (Inger, 1999; Slowinski and Wüster, 2000). In the genus *Cyrtodactylus* this has been exacerbated by the gross similarity in color pattern of nearly all species (mid-brown with darker blotches or bands, often with whitish borders) which has made identifications difficult for

non-specialists. Further, some of the species endemic to the region are known only from a few specimens, or have been plagued by confusion in the literature. A case in point is *Cyrtodactylus feae*. This species was described by Boulenger (1893) from Puepoli, in the Karen Hills of south-eastern Burma based on one male specimen collected by Leonardo Fea in 1886. Annandale (1905a) considered three female specimens from "Sinkip Island, East Sumatra" to be referable to the species, but subsequently (Annandale 1913) reidentified these specimens as juvenile *C. consobrinus* (see also de Rooij 1915). Smith (1935) reexamined the type and concluded that it was a female, not a male, and determined that Boulenger's (1893) count of 32 continuous precloacal-femoral pores was incorrect. Instead Smith regarded the enlarged precloacal and femoral scales to be merely pitted, not perforated by pores. Constable (1949) followed Smith's interpretation and referred a specimen from Calcutta, India to *C. feae*. However, both this specimen's provenance and its supposed resemblance to *C. intermedius* strongly suggest that this specimen is not conspecific with that described and figured by Boulenger (1893). No additional specimens that are unambiguously referable to *C. feae* have since been collected.

Similar confusion regarding precloacal and femoral pore condition is rampant in *Cyrtodactylus*. My examination of several hundred specimens suggests that some early authors, working with hand lenses or inferior low magnification microscopes with poor lighting, may have overlooked tiny pores and thus mischaracterized certain taxa. Other features that have been widely used in differentiating members of the genus, including postmental scale condition and the state of subcaudal scales, while easily observed, appear to have been described differently enough by different authors as to render literature accounts unreliable for comparative purposes. To assist in the identification of future collections from Myanmar, I provide the following key to the 16 species thus far recorded from the country.

#### Key to the Species of *Cyrtodactylus* Occurring in Myanmar

- 1a. Deep precloacal (pubic) sulcus present . . . . . *C. rubidus*
- 1b. Precloacal sulcus absent . . . . . 2
- 2a. Greatly enlarged pore-bearing scale posterior to main precloacal pore row . . . *C. chrysopylos*
- 2b. No enlarged pore-bearing scale. . . . . 3
- 3a. Ventral scales enlarged, equal in number to dorsal tubercle rows . . . . . *C. aequalis*
- 3b. Scale rows across mid-belly substantially exceed dorsal tubercle rows . . . . . 4
- 4a. Males<sup>2</sup> with precloacal pores only (or precloacal pores barely reaching thigh base) . . . . . 5
- 4b. Males with diastema between precloacal and femoral pore series. . . . . 14
- 5a. Femoral scales enlarged . . . . . 6
- 5b. Femoral scales not enlarged . . . . . 10
- 6a. Dark dorsum patterned with light markings . . . . . 7
- 6b. Light dorsum patterned with dark markings. . . . . 8
- 7a. Light markings arranged transversely, head with light reticulations. . . . . *C. feae*
- 7b. Light markings arranged longitudinally, head without reticulations . . . . . *C. oldhami*
- 8a. Dorsal pattern of thin dark bands with light edging . . . . . 9
- 8b. Dorsal pattern of dark spots or regular blotches . . . . . *C. peguensis*

<sup>2</sup> Female condition only known for *C. wakeorum*

9a. Dorsum of head unpatterned . . . . .	<i>C. wakeorum</i>
9b. Dorsum of head with dark markings . . . . .	<i>C. consobrinoides</i>
10a. Median subcaudal scales enlarged to form transverse plates . . . . .	<i>C. variegatus</i>
10b. No median subcaudal plates . . . . .	11
11a. Digits very short, subcaudal scalation granular . . . . .	<i>C. brevidactylus</i>
11b. Digits moderately long, subcaudal scales much larger than dorsal tail scales . . . . .	12
12a. Precloacal pores in a strongly angled series, recessed in a shallow groove (males only); females with precloacal pores present . . . . .	<i>C. gansi</i>
12b. Precloacal pores less acutely angled, not recessed; pores absent in females . . . . .	13
13a. Dorsal pattern of paired dark rectangular markings with white punctuations or bands, light bands on tail much narrower than dark . . . . .	<i>C. ayeyarwadyensis</i>
13b. Dorsal pattern not as above, light and dark tail bands subequal . . . . .	<i>C. khasiensis</i>
14a. Large (SVL to over 100 mm), digits elongate . . . . .	15
14b. Small (SVL < 56 mm), digits relatively short . . . . .	<i>C. annandalei</i>
15a. Precloacal pores 15, femoral pores 16–19 per thigh, dorsal pattern of transverse dark bands . . . . .	<i>C. russelli</i>
15b. Precloacal pores 9–11, femoral pores 11–12 per thigh, dorsal pattern of regular, paired dark blotches . . . . .	<i>C. slowinskii</i>

To date a complete revision of *Cyrtodactylus* has not been attempted, nor have any phylogenetic analyses of the group been undertaken. Phenetic similarity, however, suggests some probable affinities among the species of Myanmar. It is clear that *C. russelli* is closely allied to *C. slowinskii*. These are the only two species in Myanmar to exceed 100 mm SVL and the two share similarities in precloacal and femoral pore configuration as well as color pattern. Together these species are probably part of a more widespread clade of large-bodied, long-fingered forms that includes *C. consobrinus* and other species extending from southeast Asia through the Indoaustralian Archipelago to the western Pacific. Although less similar in overall appearance, *C. aequalis* and *C. chrysopylos* also have elongate digits, relatively large body size and well-demarcated, denticulate ventrolateral body folds and are probably members of this same clade.

*Cyrtodactylus wakeorum* is phenetically very similar to *C. consobrinoides* and is probably closely related to this form. *Cyrtodactylus annandalei* is also somewhat similar in appearance to *C. consobrinoides*, and to *C. peguensis*, but its pore configuration is substantially different from either. All of these species are relatively small bodied and have moderately short digits and weakly-developed ventrolateral folds, without denticulate margins. *Cyrtodactylus ayeyarwadyensis* and *C. gansi* are very similar to *C. khasiensis* with respect to size, body proportion, scalation, and general color pattern. These species almost certainly are each others closest relatives and replace one another geographically from the northern Assam border ranges (*C. khasiensis*), to the Chin Hills (*C. gansi*), to the lowlands west and south of the Rakhine Yoma (*C. ayeyarwadyensis*).

The distribution of the seven new species of *Cyrtodactylus*, and of all geckos in Myanmar, is largely a function of collecting effort. That so many new taxa should be discovered in a short period reflects both the intensive collecting effort of the Myanmar Herpetological Survey and the fact that the Survey has collected chiefly in areas that have not previously been explored herpetologically. For example, the collections made and reported on by Theobald (1868) were chiefly from Pegu (Bago) and Tenasserim (Tanintharyi). Even Fea, who traveled extensively in both Upper and

Lower Burma, including Tenasserin, Carin (now Kayin) State, Mandalay, and Bhamo (Banmo) in the Cactin (Kakhien) Mountains near the Yunnan border (Boulenger 1887a, 1887b, 1888, 1893; Fea 1897; Hallermann et al. 2002), collected almost exclusively east of the Ayeyarwady River.

It is not surprising that the only one of the species for which several localities over a distance of more than 100 km exist is the lowland form *C. ayeyarwadyensis*. Although the additional localities for the other taxa may be expected, it seems likely that most *Cyrtodactylus* in Myanmar will be found to be restricted to individual montane areas or hill ranges. This is almost certainly the case for *C. brevidactylus*, which occurs on the isolated Mt. Popa in north-central Myanmar, but probably also applies to species inhabiting the north-to-south running ranges both east and west of the central dry zone, which is itself an apparent area of endemism (Bauer 2002). Despite the intensive work of the Myanmar Herpetological Survey, Annandale's (1905b) statement that "the country between northern Assam and southern Tenasserim is one . . . which even the systematist has not yet exhausted the vertebrate zoology" is as true today as it was nearly a century ago.

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**Species Revision of the Coelotine Spider Genera  
*Bifidocoelotes*, *Coronilla*, *Draconarius*, *Femoracoelotes*,  
*Leptocoelotes*, *Longicoelotes*, *Platocoelotes*, *Spiricoelotes*,  
*Tegeocoelotes*, and *Tonsilla* (Araneae: Amaurobiidae)**

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The following coelotine genera from East Asia are revised: *Bifidocoelotes* Wang, with two species; *Coronilla* Wang, with five species, including two new species (*C. libo* and *C. subsigillata*) and one new synonym (the species *C. yanling* Zhang and Yin, 2001 is a junior synonym of *C. gemata*); *Draconarius* Ovtchinnikov, with 86 species, including 24 new species (*D. baxiantaiensis*, *D. haopingensis*, *D. episomos*, *D. absentis*, *D. agrestis*, *D. capitulatus*, *D. curiosus*, *D. disgregus*, *D. dissitus*, *D. dubius*, *D. griswoldi*, *D. incertus*, *D. linxiaensis*, *D. nudulus*, *D. parabrunneus*, *D. paraterebratus*, *D. patellabifidus*, *D. pseudobrunneus*, *D. pseudocapitulatus*, *D. pseudowuermlii*, *D. rotundus*, *D. simplicidens*, *D. tibetensis*, and *D. yichengensis*), five new synonyms (the species *D. parawudangensis* Zhang, Zhu and Song, 2002 is a junior synonym of *D.*

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*wudangensis*, the species *D. sinualis* (Chen, Zhao and Wang, 1991) is a junior synonym of *D. lutulentus*, the species *Coelotes rufuloides* Zhang, Peng and Kim, 1997 is a junior synonym of *D. rufulus*, the species *Coelotes shuangpaiensis* Peng, Gong and Kim, 1996 is a junior synonym of *D. digitusiformis*, and the species *D. baccatus* (Wang, 1994) is a junior synonym of *D. neixiangensis*, and 37 new combinations, all transferred from genus *Coelotes* (*D. acidentatus* (Peng and Yin, 1998), *D. adligansus* (Peng and Yin, 1998), *D. altissimus* (Hu, 2001), *D. amygdaliformis* (Zhu and Wang, 1991), *D. argenteus* (Wang et al., 1990), *D. bituberculatus* (Wang et al., 1990), *D. brunneus* (Hu and Li, 1987), *D. carinatus* (Wang et al., 1990), *D. chaigiaoensis* (Zhang, Peng and Kim, 1997), *D. denisi* (Schenkel, 1963), *D. digitusiformis* (Wang et al., 1990), *D. everesti* (Hu, 2001), *D. funiushanensis* (Hu, Wang and Wang, 1991), *D. gyrimiformis* (Wang and Zhu, 1991), *D. hangzhouensis* (Chen, 1984), *D. himalayaensis* (Hu, 2001), *D. hui* (Dankittipakul and Wang), *D. huizhunesis* (Wang and Xie, 1988), *D. jiangyongensis* (Peng, Gong and Kim, 1996), *D. linzhiensis* (Hu, 2001), *D. magniceps* (Schenkel, 1936), *D. nanyuensis* (Peng and Yin, 1998), *D. ornatus* (Wang et al., 1990), *D. penicillatus* (Wang et al., 1990), *D. pervicax* (Hu and Li, 1987), *D. picta* (Hu, 2001), *D. qingzangensis* (Hu, 2001), *D. quadratus* (Wang et al., 1990), *D. rufulus* (Wang et al., 1990), *D. streptus* (Zhu and Wang, 1994), *D. strophadatus* (Zhu and Wang, 1991), *D. subitanus* (Hu, 1992), *D. syzygiatus* (Zhu and Wang, 1994), *D. terebratus* (Peng and Wang, 1997), *D. tryblionatus* (Wang and Zhu, 1991), *D. uncinatus* (Wang et al., 1990), and *D. yadongensis* (Hu and Li, 1987); *Femoracoelotes* Wang, with two species; *Leptocoelotes* Wang, with two species; *Longicoelotes* Wang, with three species, including two new combinations, all transferred from genus *Coelotes* (*L. kulianganus* (Chamberlin, 1924) and *L. senkakuensis* (Shimojana, 2000)); *Platocoelotes* Wang, with five species, including one new species (*P. kailiensis*); *Spiricoelotes* Wang, with three species, including one new species (*S. pseudozonatus*); *Tegecoelotes* Ovtchinnikov, with five species; and *Tonsilla* Wang and Yin, with seven species, including one new species (*T. makros*) and two new combinations, all transferred from genus *Coelotes* (*T. lyratus* (Wang et al., 1990) and *T. tautispinus* (Wang et al., 1990)).

Coelotine spiders are endemic to the Holarctic region, where they are distributed from eastern North America, Europe, middle Asia, to East Asia, and comprise at least 277 species (Platnick 2000–2002; Wang 2002). Wang (2002) provided a generic revision and recognized 20 genera. The ongoing species revision by the author shows a great coelotine species diversity, particularly in East Asia.

The species of the North American genus *Wadotes* Chamberlin, 1925, with 11 described species, were revised by Bennett (1987) and those of the Himalayan genus *Himalcoelotes* Wang, 2002, with 10 described species, were revised by Wang (2002). In the present study, 10 East Asian genera are revised: they are *Bifidocoelotes* Wang, 2002; *Coronilla* Wang, 1994; *Draconarius* Ovtchinnikov, 1999; *Femoracoelotes* Wang, 2002; *Leptocoelotes* Wang, 2002; *Longicoelotes* Wang, 2002; *Platocoelotes* Wang, 2002; *Spiricoelotes* Wang, 2002; *Tegecoelotes* Ovtchinnikov, 1999; and *Tonsilla* Wang and Yin, 1992.

## MATERIALS AND METHODS

As coelotines are somatically relatively uniform, descriptions of the new species record only variable structures, such as chelicerae, eyes, and male and female genitalic structures, with special emphasis on genitalic structures in redescriptions of known species. Eyes, legs, and body lengths are given in the new species descriptions.

All measurements are in mm. Eye sizes are measured as the maximum diameter from either dorsal or frontal views. Leg measurements are given as: total length (femur, patella + tibia, metatarsus, tarsus). All scale lines are 0.2 mm length except where indicated otherwise.

**ABBREVIATIONS.**— ALE – anterior lateral eyes; AME – anterior median eyes; PLE – posterior or lateral eyes; PME – posterior median eyes; RTA – retrolateral tibial apophysis.

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L. Leibensperger.
- MNHN – Museum National d'Histoire Naturelle, Paris, France. C. Rollard
- NBUMS – Norman Bethune University of Medical Sciences, Changchun, China. J.C. Gao and C.D. Zhu
- NHMB – Naturhistorisches Museum Basel, Basel, – Switzerland. A. Hänggi
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- SZM – Siberian Zoological Museum, Novosibirsk, Russia. D.V. Logunov
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- USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.  
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- ZSM – Zoologische Staatssammlung, München, Germany. E. Karl
- IZI – Institute of Zoology, Innsbruck, Austria. K. Thaler

Institution abbreviations used in this paper also include:

- SDU – Shandong University, Jinan, China.

## TAXONOMY

**Genus *Bifidocoelotes* Wang, 2002**

*Bifidocoelotes* Wang, 2002:37 (type species, by original designation, *Coelotes bifida* Wang, Tso and Wu, 2001, from Taiwan).

**DIAGNOSIS.**— The female can be distinguished from other coelotines by having the single, bifurcate epigynal tooth. The male is similar to *Asiacoelotes* and *Draconarius* by having the elongated cymbial furrow and long embolus, but differs from *Asiacoelotes* by the presence of a conductor dorsal apophysis and from *Draconarius* by the broad, bifurcate conductor and the small median apophysis (Figs. 1–2).

**PHYLOGENETIC PLACEMENT.**— Remains unresolved; with genera *Draconarius*, *Asiacoelotes*, and the *Platocoelotes* + *Spiricoelotes* clade, supported by the strongly elongated spermathecal tubes, well-developed cymbial furrow, long embolus, and posteriorly originating embolic base (Wang, 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— China (Map 1).

**COMPOSITION.**— 2 species:

1. *Bifidocoelotes bifidus* (Wang, Tso and Wu, 2001)
2. *Bifidocoelotes primus* (Fox, 1937)

***Bifidocoelotes bifidus* (Wang, Tso and Wu, 2001)**

Figures 1A–D; Map 1

*Coelotes bifida* Wang, Tso and Wu, 2001:128, figs. 1–10 (female holotype and male paratype from Nantou, Taiwan, in THU, examined).

*Bifidocoelotes bifida*: Wang, 2002:38, figs. 86–100.

**DIAGNOSIS.**— Distinguished from *B. primus* by the shorter epigynal bifurcation (less than ½ of the total length), the strongly developed copulatory ducts, the medially situated spermathecal heads, and the widely separated, longitudinally elongated spermathecae (Figs. 1A–D).

**DESCRIPTION.**— Described by Wang, Tso and Wu (2001) and Wang (2002). Chelicerae with three promarginal and two retromarginal teeth. Female epigynum with single, long, slightly bifurcate epigynal tooth (less than ½ total length); atrium small, anteriorly situated, near base of epigynal tooth; copulatory ducts long, strongly convoluted mesad of spermathecae, and slightly extending laterad of spermathecae; spermathecal heads small, situated anteriorly, close together; spermathecal bases widely separated, stalks elongated, slightly convoluted, widely separated and anteriorly converging (Figs. 1A–B). Male palp with patellar apophysis large, with slightly curved apex; RTA long; lateral tibial apophysis small; cymbial furrow longer than half cymbial length; conductor broad, more or less spiraled, with bifurcate apex; conductor with dorsal edge bearing broad membranous extension, dorsal apophysis small, lamella well developed; embolus posterior in origin, long, slender; median apophysis small, spoon-like (Figs. 1C–D).

**DISTRIBUTION.**— China (Taiwan) (Map. 1).

**MATERIAL EXAMINED.**— CHINA: Taiwan: Nantou County, Huei-Sun Experimental Forest, elevation 1680m, March 31, 1998, female holotype (Hai-Yin Wu; THU, THU-Ar-990017); Nantou County, Huei-Sun Experimental Forest, March 31, 1998, 1 male paratype (Hai-Yin Wu; THU, THU-Ar-990020); Nantou County, Huei-Sun Experimental Forest, elevation 1680m, March 31, 1998, 1 male (Hai-Yin Wu, THU, THU-Ar-990019); Nantou County, Huei-Sun Experimental Forest, elevation 1675m, March 31, 1998, 1 male (Hai-Yin Wu, THU, THU-Ar-990026); Nantou

County, Hwei-Sun Experimental Forest, elevation 1550m, March 31, 1998, 1 female (Hai-Yin Wu, THU, THU-Ar-990027).

***Bifidocoelotes primus* (Fox, 1937)**

Figures 2A–B; 97G; Map 1

*Wadotes primus* Fox, 1937:1, figs. 1–2 (female holotype and female paratype from Hong Kong, China, in AMNH and USNM, examined). Bennett, 1987:126, figs. 109–110.— Song, Zhu and Chen, 1999:395.

*Bifidocoelotes primus*: Wang, 2002:37.

**DIAGNOSIS.**— Distinguished from *B. bifidus* by the strongly bifurcate epigynal tooth (bifurcation more than  $\frac{1}{2}$  total length), the short copulatory ducts, the laterally situated, medially extending spermathecal heads, the closely situated spermathecae, and the transversely extending spermathecal bases (Figs. 2A–B).

**DESCRIPTION.**— Described by Fox (1937). Chelicerae with three promarginal and two retro-marginal teeth. Female epigynum with single bifurcate tooth, bifurcation more than one half total length; atrium broad; epigynal hoods deep, situated laterad of atrium; copulatory ducts short; spermathecal heads long, slender, originating laterad of spermathecae, anteriorly extending and converging; spermathecal bases large, close together, laterally extending, stalks broad, convoluted, situated close together (Figs. 2A–B).

**DISTRIBUTION.**— China (Hong Kong) (Map. 1)

**MATERIAL EXAMINED.**— CHINA: Hong Kong: Tingping Mt., October 14, 1997, 1 female (X. P. Wang, IZB); Hong Kong, female holotype (AMNH); Hong Kong, late January, 1920, 1 female paratype (Bassett Digby, USNM).

## **Genus *Coronilla* Wang, 1994**

*Coronilla* Wang, 1994: 281 (type species, by original designation, *Coronilla gemata* Wang, 1994, from China).— Platnick, 1997:667;— Wang, 2002:61.

**DIAGNOSIS.**— The male can be distinguished from all other coelotine genera except *Femoracoelotes* by the absence of a lateral tibial apophysis, and from *Femoracoelotes* by the absence of a femoral apophysis and the presence of two patellar apophyses. The female can be recognized by the broad atrium, the presence of transversely extending atrial carina, and the absence of epigynal teeth (Figs. 3–6).

**PHYLOGENETIC PLACEMENT.**— The presence of four cheliceral retromargin teeth suggests *Coronilla* is the sister group of *Femoracoelotes* from Taiwan; together they form the sister group of all other coelotines (Wang, 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— China, Vietnam (Map 2).

**COMPOSITION.**— 5 species, including 2 new species and 1 new synonym:

1. *Coronilla gemata* Wang, 1994  
*Coelotes huangsangensis* Peng et al., 1998  
*Coelotes yoshikoe* Nishikawa, 1995  
*Coronilla yanling* Zhang and Yin, 2001, NEW SYNONYMY
2. *Coronilla libo*, sp. nov.
3. *Coronilla mangshan* Zhang and Yin, 2001
4. *Coronilla sigillata* Wang, 1994
5. *Coronilla subsigillata*, sp. nov.

**Key To the Species of the Genus *Coronilla***

1. Male (those of *C. subsigillata* unknown) ..... 2  
    Female (those of *C. libo* unknown) ..... 5
2. Patella with three apophyses ..... *mangshan*  
    Patella with two apophyses ..... 3
3. Median apophysis spiraled; conductor simple, not bifurcate, without ventral apophysis (Fig. 4B) ..... *libo*  
    Median apophysis not spiraled; conductor either bifurcate (Fig. 5D) or with ventral apophysis (Fig. 3D) ..... 4
4. Ventral patellar apophysis slender; conductor with large ventral apophysis; conductor dorsal apophysis small, not toothed (Figs. 3C-E) ..... *gemata*  
    Ventral patellar apophyses broad; conductor with small ventral apophysis; Conductor dorsal apophysis large, toothed (Figs. 5C-D) ..... *sigillata*
5. Spermathecae with laterally extending apophyses; spermathecal heads short, broad (Fig. 3B) ..... *gemata*  
    Spermathecae without laterally extending apophyses; spermathecal heads long, slender (Figs. 5B, 6B) ..... 6
6. Copulatory ducts rounded, anteriorly situated ..... *mangshan*  
    Copulatory ducts posteriorly extending ..... 7
7. Copulatory ducts with broad, slightly lobed posterior edges; spermathecal heads originating dorsally (Fig. 5B) ..... *sigillata*  
    Copulatory ducts with narrow, non-lobed posterior edges; spermathecal heads originating ventrally (Fig. 6B) ..... *subsigillata*

***Coronilla gemata* Wang, 1994**

Figures 3A–E; Map 2

*Coronilla gemata* Wang, 1994:281, figs. 1–5 (female holotype and male allotype from Mt. Zhangjiajie, Dayong, Hunan, China, in HTU, examined).— Song, Zhu and Chen, 1999:389, figs. 229G–H, K–M;— Wang, 2002:61, figs. 158–180.

*Coelotes yoshikoe* Nishikawa, 1995:141, figs. 1–8 (types from Vinh Phu Prov., Vietnam, in NSMT, not examined).

*Coelotes huangsangensis* Peng et al., 1998:77, figs. 1–6 (female holotype and male allotype from Huangsang, Suining, Hunan, China, in HBI, examined).

*Coronilla yanling* Zhang and Yin, 2001:489, figs. 8–11 (male holotype and 1 male paratype from Taoyuan-dong, Yanling, Hunan, China, in HBI, not examined). NEW SYNONYMY.

**DIAGNOSIS.**— The male can be distinguished from *C. libo* by the presence of broad conductor ventral apophysis and from *C. sigillata* by the slender patellar ventral apophysis. The female can be recognized by the presence of spermathecal lateral apophyses and the anteriorly situated spermathecal heads (Figs. 3A–E).

**DESCRIPTION.**— Described by Wang (1994) and Wang (2002). Chelicerae with three promarginal and four retromarginal teeth. Female epigynum without teeth; atrium large, carina broad, transversely extending; copulatory ducts large; spermathecal heads short, situated anteriorly; sper-

mathecal bases transversely extending, situated close together; spermathecal stalks broad, with lateral apophyses (Figs. 3A–B). The male palp with two patellar apophyses, ventral slender and long (occasionally short), dorsal short and strong; RTA slightly shorter than tibia; lateral tibial apophysis absent; cymbial furrow short; conductor short, ventral apophysis long, broad, anteriorly curved; conductor dorsal apophysis large; median apophysis slender, with slightly curved apex (Figs. 3C–E).

**DISTRIBUTION.**— China (Hunan, Sichuan) and VIETNAM (Vinh Phu) (Map 2).

**MATERIAL EXAMINED.**— CHINA: Hunan: Dayong, Mt. Zhangjiajie, November 5, 1985, female holotype, 6 female and 8 male paratypes (J.F. Wang, HTU); Tianpingshan, October 16, 1986, 4 females and 4 males (J.F. Wang, HTU); Suining, Huangsang, October 14, 1996, female holotype and male paratype of *C. huangsangensis* Peng et al., 1998 (M.X. Liu, HBI). Sichuan: E-mei-shan, September 27, 1975, 2 females (C.D. Zhu, NBUMS, 75–2172); Chongqing, September 26, 1997, molted to adult later October, 1 male (X.P. Wang, AMNH).

***Coronilla libo* Wang, sp. nov.**

Figures 4A–B; Map 2

**TYPES.**— The male holotype, 2 male paratypes from Libo, Guizhou, China (October 5, 1997; X. P. Wang), deposited in AMNH (holotype) and IZB (paratypes).

**ETYMOLOGY.**— The specific name refers to the type locality.

**DIAGNOSIS.**— The male can be distinguished from *C. gemata* and *C. sigillata* by the simple conductor (not bifurcate, without ventral apophysis), and the strongly spiraled median apophysis (Figs. 4A–C).

**MALE.**— Total length 8.20. Carapace 4.20 long, 2.96 wide. Cheliceral promargin with three teeth, retromargin four (occasionally five). Eye sizes and interdistances: AME 0.20, ALE 0.24, PME 0.20, PLE 0.21, AME-AME 0.10, AME-ALE 0.05, PME-PME 0.13, PME-PL 0.19, ALE-PL 0.04, AME-PME 0.18. Clypeal height 0.30. Leg measurements: I: 14.7 ( 4.00, 4.96, 3.84, 1.88); II: 13.1 ( 3.60, 4.41, 3.40, 1.64); III: 11.6 ( 3.28, 3.80, 3.00, 1.48); IV: 14.6 ( 4.12, 4.72, 4.04, 1.68). Male palp with two patellar apophyses, ventral one relatively long and dorsally curved, dorsal one short; RTA slightly shorter than tibia; conductor slender, without ventral apophysis; conductor dorsal apophysis broad; median apophysis slender, long, with spiraled apex (Figs. 4A–C).

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Guizhou) (Map 2).

**OTHER MATERIAL EXAMINED.**— None.

***Coronilla mangshan* Zhang and Yin, 2001**

Map 2

*Coronilla mangshan* Zhang and Yin, 2001:487, figs. 1–7 (male holotype, 1 male and 2 female paratypes from Mangsha, Yizhang, Hunan, China, in HBI, not examined).

**DIAGNOSIS.**— The male can be distinguished from other species by the presence of three patellar apophyses and the female by the rounded, anteriorly situated copulatory ducts.

**DESCRIPTION.**— Described by Zhang and Yin (2001). Cheliceral promargin with three teeth, retromargin four. Female epigynum lacking teeth; atrium large; posterior margin strongly extending; copulatory ducts broad, rounded, anteriorly situated; spermathecal heads small, situated medially on spermathecae, close together; spermathecal bases small, slightly separated; spermathecal

stalks close together, anteriorly diverging. Male palp with three patellar apophyses; conductor with ventral apophysis short, dorsal apophysis broad; median apophysis slender, slightly spiraled.

**DISTRIBUTION.**— China (Hunan) (Map 2).

**MATERIAL EXAMINED.**— None.

### *Coronilla sigillata* Wang, 1994

Figures 5; Map 2

*Coronilla sigillata* Wang, 1994: 282, figs. 6–10 (female holotype, 2 male paratypes from Mt. Tianmushan, Zhejiang, China, in HTU, examined).— Song, Zhu and Chen, 1999:389, figs. 229I–J, L–M.

**NOTES.**— Two male (one without palp) and three female types are examined from the same vial labeled as *C. sigillata*, but only one female matches the illustrations of the holotype female (Wang, 1994: figs. 9, 10). The two other females have quite different genitalic morphology and are treated in this study as a new species, *C. subsigillata* sp. nov. All specimens were collected from October 21 to October 23, 1974. It is possible that two *Coronilla* species exist in this location (Mt. Tianmushan). Whether the males are *C. sigillata* or *C. subsigillata* sp. nov. is uncertain. Here in this paper, the male specimens examined provisionally associated with *C. sigillata*.

**DIAGNOSIS.**— The male can be distinguished from other species by one strongly developed and one much reduced patellar apophysis and the broad, toothed conductor dorsal apophysis (Figs. 5C–E). The female can be recognized from *C. subsigillata* by the posteriorly notched copulatory ducts and the differences between their spermathecal head shapes (Figs. 5A–B).

**DESCRIPTION.**— Described by Wang (1994). Cheliceral promargin with three teeth, retromargin four. Epigynal teeth absent; atrium large, carina broad, transversely extending; posterior margin strongly extending; copulatory ducts broad, with notched posterior end; spermathecal heads long, slender, situated dorsally on spermathecae; spermathecal bases small, situated close together; spermathecal stalks long, wide apart anteriorly and converging posteriorly (Figs. 5A–B). Male palp with two patellar apophyses, ventral long and strong, dorsal short; RTA as long as tibial length; conductor with ventral apophysis long, dorsal apophysis broad, with sharp anterior tooth and rounded posterior process; median apophysis relatively broad, with slightly curved apex (Figs. 5C–E).

**DISTRIBUTION.**— China (Zhejiang) (Map 2).

**MATERIAL EXAMINED.**— CHINA: Zhejiang: Mt. Tiamushan, October 21–23, 1974, female holotype and 2 male paratypes (J.F. Wang, HTU).

### *Coronilla subsigillata* Wang, sp. nov.

Figures 6, Map 2

**TYPES.**— Female holotype from Tianmushan, Zhejiang, China (October 21–23, 1974; J.F. Wang), deposited in HTU.

**ETYMOLOGY.**— The specific name refers to its similarity to *C. sigillata*.

**DIAGNOSIS.**— This new species is similar to *C. sigillata* but can be distinguished by the less expanded posterior atrial margin, the posteriorly extending, non-notched copulatory ducts, and the ventrally situated spermathecal heads of the female (Figs. 6A–B).

**FEMALES.**— Total length 12.6. Carapace 5.80 long, 4.00 wide. Cheliceral promargin with three teeth, retromargin four. Eye sizes and interdistances: AME 0.24, ALE 0.27, PME 0.22, PLE 0.23, AME-AME 0.15, AME-ALE 0.15, PME-PME 0.29, PME-PLE 0.40, ALE-PLE 0.12, AME-PME



0.29. Clypeal height 0.42. Leg measurements: I: 15.3 ( 4.36, 5.36, 3.60, 2.00); II: 13.5 ( 3.92, 4.64, 3.32, 1.64); III: 12.1 ( 3.48, 3.96, 3.12, 1.52); IV: 14.9 ( 4.24, 5.00, 3.96, 1.72). Epigynal teeth absent; atrium large, carina broad, transversely extending; epigynum with posterior margin slightly extending posteriorly; copulatory ducts broad, with extending, unnotched posterior ends; spermathecal heads ventrally situated, mostly covered by copulatory ducts from dorsal view; spermathecal bases small, situated close together; spermathecal stalks long, laterally extending (Figs. 6A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 2)

**OTHER MATERIAL EXAMINED.**— CHINA: Zhejiang: Mt. Tiamushan, October 21–23, 1974, 1 female (not in good condition) (J.F. Wang, HTU).

### Genus *Draconarius* Ovtchinnikov, 1999

*Draconarius* Ovtchinnikov, 1999:70 (type species, by original designation, *Draconarius venustus* Ovtchinnikov, 1999 from Tadzhikistan).— Wang, 2002:66.

**DIAGNOSIS.**— Similar to *Asiacoelotes* in having an elongated cymbial furrow (longer than half cymbial length) but can be distinguished by the posteriorly originating copulatory ducts and the presence of a conductor dorsal apophysis; similar to *Coelotes* in having a patellar apophysis and a conductor dorsal apophysis but can be distinguished by the elongated cymbial furrow (more than half cymbial length), the long, posteriorly extending embolus, and the elongated median apophysis of male and by the large copulatory ducts and the long spermathecae of female (Figs. 7–69).

**PHYLOGENETIC PLACEMENT.**— Remains unresolved with *Bifidocoelotes*, *Asiacoelotes*, and the *Platocoelotes*+*Spiricoelotes* clade. Together they are supported by the strongly elongated spermathecal tubes, the well-developed cymbial furrow, the long embolus, and the posteriorly originating embolic base (Wang, 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— Tadzhikistan, Bhutan, Nepal, China, Korea (Map 33).

**GENITALIC VARIATIONS.**— Patellar apophysis present in general, but can be absent in some species; RTA long, occupying most of tibial length, or occasionally short, about half tibial length; lateral tibial apophysis present; cymbial furrow long, broad, occupying more than half cymbial length in most species, but can be short, less than half cymbial length; conductor simple, with dorsal apophysis; conductor lamella large in general, or reduced in some species; median apophysis spoon-like, strongly elongated as in most species, but may be simple, not spoon-like, or absent; embolus long, posterior in origin in most species, or short, prolateral in origin in others. Epigynal teeth short in almost all species, but long as in *huizhunesis* group; epigynal teeth widely separated in most species, but may be closely and anteriorly situated, or absent in few others; atrium small, situated posteriorly in most species, but may vary in its shape and position in some species; copulatory ducts originated posteriorly, extending mesad of spermathecae in general, but may be extending laterad of spermathecae, extending anteriorly, looping around spermathecae, or strongly looped laterad of spermathecae; spermathecae broad, long in general, but can be short, rounded as in *gurkha* group species.

**SPECIES GROUPS.**— Many *Draconarius* species are described in recent years with only male or female. Most of those described with both male and female are only based on a limited number of individuals and some might be incorrectly matched. As a result, a phylogenetic analysis at this moment can hardly be achieved and in this study 35 of the 86 species are grouped only arbitrarily based on the female genitalic characteristics; the other 51 are unplaced.

**COMPOSITION.**— 86 species, including 24 new species, 5 new synonyms, and 37 new combinations. Among them, 35 species are grouped into 7 species groups according to female genitalia, and the other 51 species remain unplaced:

### **The *venustus* group species**

The female epigynum with epigynal teeth short, may be anteriorly and closely situated (Fig. 17A), or medially situated and widely separated (Figs. 13A, 67A), or occasionally lacking (Fig. 62A); copulatory ducts short, situated mesad of spermathecae; spermathecae broad, with short, broad anterior expansion; spermathecal heads medially situated (Figs. 13B, 67B). Chelicerae with three promarginal and two retromarginal teeth. Widespread in East Asia.

1. *Draconarius aspinatus* (Wang et al., 1990)
2. *Draconarius baxiantaiensis*, sp. nov.
3. *Draconarius calcariformis* (Wang, 1994)
4. *Draconarius colubrinus* Zhang, Zhu and Song, 2002
5. *Draconarius coreanus* (Paik and Yaginuma, 1969) (In Paik, Yaginuma, and Namkung, 1969)
6. *Draconarius davidi* (Schenkel, 1963)
7. *Draconarius funiushanensis* (Hu, Wang and Wang, 1991), NEW COMBINATION (from *Coelotes*)
8. *Draconarius gyriniformis* (Wang and Zhu, 1991), NEW COMBINATION (from *Coelotes*)
9. *Draconarius hui* (Dankittipakul and Wang, 2003), NEW COMBINATION (from *Coelotes*).

Replacement name for preoccupied. *Coelotes wangi* Hu, 2001

10. *Draconarius linzhiensis* (Hu, 2001), NEW COMBINATION (from *Coelotes*)
11. *Draconarius picta* (Hu, 2001), NEW COMBINATION (from *Coelotes*)
12. *Draconarius qingzangensis* (Hu, 2001), NEW COMBINATION (from *Coelotes*)
13. *Draconarius stemmleri* (Brignoli, 1978)
14. *Draconarius striolatus* (Wang et al., 1990)
15. *Draconarius trifasciatus* (Wang and Zhu, 1991)
16. *Draconarius venustus* Ovtchinnikov, 1999
17. *Draconarius wudangensis* (Chen and Zhao, 1997)

*Draconarius parawudangensis* Zhang, Zhu and Song, 2002, NEW SYNONYMY

18. *Draconarius yadongensis* (Hu and Li, 1987), NEW COMBINATION (from *Coelotes*)
19. *Draconarius yosiianus* (Nishikawa, 1999)

### **The *labiatus* group species**

The female epigynum with epigynal teeth short, anteriorly and closely situated (Figs. 37A, 66A); copulatory ducts short, situated mesad of spermathecae; spermathecae broad, with long, strongly convoluted anterior expansion; spermathecal heads medially situated (Figs. 37B, 66B). Chelicerae with three promarginal and two retromarginal teeth. Recorded from southern China.

20. *Draconarius labiatus* (Wang and Ono, 1998)
21. *Draconarius wenzhouensis* (Chen, 1984)

### **The *lutulentus* group species**

The female epigynum with epigynal teeth short, widely separated (Figs. 39A, 40A) or absent (Figs. 33A, 44A); copulatory ducts long, looping around spermathecae; spermathecae strongly elongated and convoluted, anteriorly converging; spermathecal heads situated distally (Figs. 33B, 39B, 40B, 44B). Chelicerae with three promarginal and three retromarginal teeth. Distributed in China and Himalayan region.

22. *Draconarius haopingensis*, sp. nov.
23. *Draconarius lutulentus* (Wang et al., 1990)
- Draconarius sinualis* (Chen, Zhao and Wang, 1991), NEW SYNONYMY
24. *Draconarius molluscus* (Wang et al., 1990)
25. *Draconarius wuermlii* (Brignoli, 1978)

**The gorkha group species**

The female epigynum with epigynal teeth short, widely separated (Figs. 30A, 32A); copulatory ducts short; spermathecae short, rounded; spermathecal heads situated anteriorly (Figs. 30B, 32B; Hu 2000, figs. 8–45.2, 8–57.2). Chelicerae with three promarginal and two retromarginal teeth. Recorded from Himalayan region.

26. *Draconarius altissimus* (Hu, 2001), NEW COMBINATION (from *Coelotes*)
27. *Draconarius episomos*, sp. nov.
28. *Draconarius gorkha* (Brignoli, 1976)  
*Coelotes lama* Brignoli, 1976
29. *Draconarius himalayaensis* (Hu, 2001), NEW COMBINATION (from *Coelotes*)
30. *Draconarius subtitianus* (Hu, 1992), NEW COMBINATION (from *Coelotes*)

**The huizhunesis group species**

The female epigynum with epigynal teeth strongly elongated, with slightly separated bases and diverging apices (Wang and Xu 1988, fig. 1; Zhu and Wang 1991, fig. 12); spermathecae long, strongly convoluted (Wang and Xu 1988, fig. 2; Zhu and Wang 1991, fig. 13). Chelicerae with three promarginal and two retromarginal teeth. Collected from eastern China.

31. *Draconarius huizhunesis* (Wang and Xie, 1988), NEW COMBINATION (from *Coelotes*)  
*C. huizhunesis*: Wang and Xie, 1988  
*C. huizhouensis*: Song, Zhu and Chen, 1999
32. *Draconarius strophadatus* (Zhu and Wang, 1991), NEW COMBINATION (from *Coelotes*)

**The terebratus group species**

The female epigynum lacking epigynal teeth (Fig. 63A); copulatory ducts broad, anteriorly extended; spermathecae short; spermathecal heads strongly elongated (Fig. 63B). Chelicerae with three promarginal and two retromarginal teeth. Distributed in eastern and southern China.

33. *Draconarius ornatus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
34. *Draconarius terebratus* (Peng and Wang, 1997), NEW COMBINATION (from *Coelotes*)

**The rufulus group species**

The female epigynum lacking epigynal teeth; atrium small, posteriorly situated (Fig. 57A); copulatory ducts broad, strongly convoluted with four to five loops laterad of spermathecae; spermathecae long; spermathecal heads small (Fig. 57B). Chelicerae with three promarginal and two retromarginal teeth. Distributed in eastern China.

35. *Draconarius rufulus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)  
*Coelotes rufuloides* Zhang, Peng and Kim, 1997, NEW SYNONYMY

**Other non-grouped species:**

36. *Draconarius absentis*, sp. nov.
37. *Draconarius acidentatus* (Peng and Yin, 1998), NEW COMBINATION (from *Coelotes*)
38. *Draconarius adligansus* (Peng and Yin, 1998), NEW COMBINATION (from *Coelotes*)
39. *Draconarius agrestis*, sp. nov.
40. *Draconarius amygdaliformis* (Zhu and Wang, 1991), NEW COMBINATION (from *Coelotes*)
41. *Draconarius arcuatus* (Chen, 1984)
42. *Draconarius argenteus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
43. *Draconarius baronii* (Brignoli, 1978)
44. *Draconarius bituberculatus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
45. *Draconarius brunneus* (Hu and Li, 1987), NEW COMBINATION (from *Coelotes*)
46. *Draconarius capitulatus*, sp. nov.
47. *Draconarius carinatus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
48. *Draconarius chaiqiaoensis* (Zhang, Peng and Kim, 1997), NEW COMBINATION (from *Coelotes*)
49. *Draconarius cheni* (Platnick, 1989)

- Coelotes saxatilis* Chen, 1984
50. *Draconarius curiosus*, sp. nov.
51. *Draconarius denisi* (Schenkel, 1963), NEW COMBINATION (from *Coelotes*)
52. *Draconarius digitusiformis* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
- Coelotes shuangpaiensis* Peng, Gong and Kim, 1996, NEW SYNONYMY
53. *Draconarius disgregus*, sp. nov.
54. *Draconarius dissitus*, sp. nov.
55. *Draconarius dubius*, sp. nov.
56. *Draconarius everesti* (Hu, 2001), NEW COMBINATION (from *Coelotes*)
57. *Draconarius griswoldi*, sp. nov.
58. *Draconarius hangzhouensis* (Chen, 1984), NEW COMBINATION (from *Coelotes*)
59. *Draconarius incertus*, sp. nov.
60. *Draconarius infulatus* (Wang et al., 1990)
61. *Draconarius jiangyongensis* (Peng, Gong and Kim, 1996), NEW COMBINATION (from *Coelotes*)
62. *Draconarius linxiaensis*, sp. nov.
63. *Draconarius magniceps* (Schenkel, 1936), NEW COMBINATION (from *Coelotes*)
64. *Draconarius nanyuensis* (Peng and Yin, 1998), NEW COMBINATION (from *Coelotes*)
65. *Draconarius neixiangensis* (Hu, Wang and Wang, 1991)
- Draconarius baccatus* (Wang, 1994), NEW SYNONYMY
66. *Draconarius nudulus*, sp. nov.
67. *Draconarius parabrunneus*, sp. nov.
68. *Draconarius paraterebratus*, sp. nov.
69. *Draconarius patellabifidus*, sp. nov.
70. *Draconarius penicillatus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
- Coelotes penicilatus*: Song, Zhu and Chen, 1999
71. *Draconarius pervicax* (Hu and Li, 1987), NEW COMBINATION (from *Coelotes*)
72. *Draconarius potanini* (Schenkel, 1963)
73. *Draconarius pseudobrunneus*, sp. nov.
74. *Draconarius pseudocapitulatus*, sp. nov.
75. *Draconarius pseudowuermlii*, sp. nov.
76. *Draconarius quadratus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
77. *Draconarius rotundus*, sp. nov.
78. *Draconarius schenkeli* (Brignoli, 1978)
79. *Draconarius simplicidens*, sp. nov.
80. *Draconarius singulatus* (Wang et al., 1990)
81. *Draconarius streptus* (Zhu and Wang, 1994), NEW COMBINATION (from *Coelotes*)
82. *Draconarius syzygiatus* (Zhu and Wang, 1994), NEW COMBINATION (from *Coelotes*)
83. *Draconarius tibetensis*, sp. nov.
84. *Draconarius tryblionatus* (Wang and Zhu, 1991), NEW COMBINATION (from *Coelotes*)
85. *Draconarius uncinatus* (Wang et al., 1990), NEW COMBINATION (from *Coelotes*)
86. *Draconarius yichengensis*, sp. nov.

**Key To Females of the Species of the Genus *Draconarius***

1. Epigynal teeth present .....	2
Epigynal teeth absent .....	52
2. Epigynal teeth long, with length at least five times width (Fig. 8A) .....	3
Epigynal teeth short, with length at most four times width (Figs. 19A; 39A) .....	5
3. Epigynal teeth with apices close together (Fig. 8A) .....	<i>acidentatus</i>
Epigynal teeth with apices widely separated .....	4

4. Spermathecae with anterior ends close together . . . . . *huizhuensis*  
Spermathecae with anterior ends widely separated. . . . . *strophadatus*

5. Epigynal teeth with bases close together, separated by less than their width (Fig. 26A)  
..... *digitusiformis*  
Epigynal teeth with bases separated at least by their width (Figs. 13A; 24A) . . . . . 6

6. Copulatory ducts expanded anteriorly anterad of spermathecae . . . . . 7  
Copulatory ducts otherwise . . . . . 14

7. Epigynal teeth situated posteriorly near epigastric furrow . . . . . *infulatus*  
Epigynal teeth situated anteriorly, widely separated from epigastric furrow . . . . . 8

8. Epigynal hoods deep, situated laterad of atrium (Figs. 56A; 58A) . . . . . 9  
Epigynal hoods shallow, situated anterad of atrium (Figs. 9A; 44A) . . . . . 10

9. Spermathecal bases widely separated, stalks long and looped; spermathecal heads situated  
anterad of spermathecae (Fig. 56B) . . . . . *rotundus*  
Spermathecal bases close together, stalks short, not looped; spermathecal heads situated laterad  
of spermathecae (Fig. 58B) . . . . . *schenkeli*

10. Epigynal teeth situated near atrial margin (Figs. 9A; 50A) . . . . . 11  
Epigynal teeth widely separated from atrial margin (Fig. 44A) . . . . . 12

11. Spermathecal stalks laterally extending; spermathecal heads surrounded by looped copulatory  
ducts (Fig. 50B) . . . . . *penicillatus*  
Spermathecal stalks short, broad, not laterally extending; spermathecal heads not surrounded  
by copulatory ducts (Fig. 9B) . . . . . *adligansus*

12. Epigynal teeth separated by less than half atrial width (Fig. 44A) . . . . . *neixiangensis*  
Epigynal teeth separated by at lease atrial width (Figs. 25A; 34A) . . . . . 13

13. Spermathecal heads short, posteriorly situated (Fig. 25B) . . . . . *denisi*  
Spermathecal heads long, anteriorly situated (Fig. 34B) . . . . . *hangzhouensis*

14. Spermathecae short, rounded, with length almost same as width (Figs. 43B; 32B) . . . . . 15  
Spermathecae elongated, with length at least twice width (Figs. 61B; 67B; 39B) . . . . . 22

15. Spermathecal heads not visible from dorsal view (Fig. 32B) . . . . . 16  
Spermathecal heads visible from dorsal view (Figs. 30B; 43B) . . . . . 17

16. Copulatory ducts broad, situated mesad of spermathecae (Fig. 60B) . . . . . *singulatus*  
Copulatory ducts not visible from dorsal view (Fig. 32B) . . . . . *gurkha*

17. Spermathecal heads situated anterad of spermathecae (Fig. 69B) . . . . . 18  
Spermathecal heads situated mesad of spermathecae (Figs. 30B; 43B) . . . . . 21

18. Epigynal teeth long, with length at least twice width; spermathecal heads situated  
anterolaterally (Fig. 69B) . . . . . *yichengensis*  
Epigynal teeth short, with length at most same as width; spermathecal heads situated  
anteriorly . . . . . 19

19. Epigynal teeth separated from atrium . . . . . *himalayaensis*  
Epigynal teeth situated near atrium. . . . . 20

20. Spermathecae close together . . . . . *altissimus*  
Spermathecae slightly separated . . . . . *subtitanus*

21. Epigynal teeth widely separated; copulatory ducts and spermathecal heads situated mesad of spermathecae (Figs. 30A–B) . . . . . *episomos*  
Epigynal teeth slightly separated; copulatory ducts originating dorsally and spermathecal heads originating ventrally on spermathecae (Figs. 43A–B) . . . . . *nanyuensis*

22. Spermathecae broad, anteriorly expanded; spermathecal heads situated medially on spermathecae (Figs. 15B; 61B; 67B) . . . . . 23  
Spermathecae otherwise . . . . . 40

23. Epigynal teeth situated anteriorly, close together (Figs. 17A; 24A) . . . . . 24  
Epigynal teeth widely separated (Figs. 13A; 67A) . . . . . 26

24. Anterior atrial margin broad, bifurcate (Fig. 17B) . . . . . *calcariformis*  
Anterior atrial margin indistinct, not bifurcate . . . . . 25

25. Spermathecal heads indistinct (Fig. 24B) . . . . . *davidi*  
Spermathecal heads distinct . . . . . *colubrinus*

26. Epigynal teeth wide apart, at least 1.5 times atrial width (Fig. 67A) . . . . . 27  
Epigynal teeth separated by atrial width or less (Fig. 13A) . . . . . 31

27. Spermathecal stalks with anterior extension not converging . . . . . *yosiiianus*  
Spermathecal stalks anteriorly converging, close together (Fig. 22B) . . . . . 28

28. Epigynal teeth situated posteriorly, near atrium . . . . . *picta*  
Epigynal teeth situated anteriorly, widely separated from atrium (Fig. 22A) . . . . . 29

29. Epigynum with a broad, membranous, transverse extension in front of atrium (Figs. 22A–B) . . . . . *coreanus*  
Epigynum without transverse extension in front of atrium (Fig. 67A) . . . . . 30

30. Spermathecal heads situated on anterior 1/3 part of spermathecae; spermathecal bases broad (Fig. 67B) . . . . . *wudangensis*  
Spermathecal heads situated on posterior 1/3 part of spermathecae; spermathecal bases narrow . . . . . *venustus*

31. Epigynal teeth situated posteriorly, at same level or posterior compared to anterior atrial margin . . . . . 32  
Epigynal teeth situated anteriorly compared to anterior atrial margin (Fig. 13A) . . . . . 35

32. Spermathecal bases close together . . . . . *funiushanensis*  
Spermathecal bases separated at least by their width . . . . . 33

33. Epigynal teeth situated at same level as anterior atrial margin . . . . . *hui*  
Epigynal teeth situated at posterior level compared to anterior atrial margin . . . . . 34

34. Spermathecal heads situated medially on spermathecae . . . . . *qingzangensis*  
Spermathecal heads situated on anterior 1/3 of spermathecae . . . . . *linzhiensis*

35. Spermathecae with anterior expansion broader than stalks (Fig. 13B) . . . . . 36  
Spermathecae with anterior expansion same or narrower than stalks (Fig. 61B) . . . . . 38

36. Epigynal teeth broad, situated slightly anterior of atrium ..... *trifasciatus*  
Epigynal teeth narrow, widely separated from atrium ..... 37

37. Anterior atrial margin expanded posteriorly (Fig.13A)..... *aspinatus*  
Anterior atrial margin not expanded posteriorly..... *gyriniformis*

38. Copulatory ducts originating medially, looped laterally (Fig. 15B) ..... *baxiantaiensis*  
Copulatory ducts originating medially, short, not looped (Fig. 61B)..... 39

39. Spermathecae widely separated, at least by their width (Fig. 61B) ..... *stemmleri*  
Spermathecae situated close together ..... *yadongensis*

40. Spermathecal stalks long, slender, extending laterally, and converging anteriorly (Fig. 39B)  
..... 41  
Spermathecal stalks broad (Figs. 19B, 51B)..... 47

41. Copulatory ducts extending along spermathecae, not looped (Fig. 21A)..... 42  
Copulatory ducts looped around spermathecae (Fig. 39B)..... 43

42. Epigynal teeth situated laterally, widely separated; spermathecal bases broad, heads long, close  
together (Figs. 36A–B) ..... *jiangyongensis*  
Epigynal teeth situated medially, moderately separated; spermathecal bases narrow, heads  
widely separated (Figs. 21A–B) ..... *cheni*

43. Epigynal teeth situated anteriorly, close together (Fig. 66A) ..... 44  
Epigynal teeth situated near atrium, widely separated (Fig. 39A) ..... 45

44. Spermathecae with anterior extension extending anteriorly; spermathecal heads not covered by  
copulatory ducts (Fig. 66B) ..... *wenzhouensis*  
Spermathecae with anterior extension extending medially; spermathecal heads covered by cop-  
ulatory ducts (Fig. 37B) ..... *labiatus*

45. Epigynal teeth separated by less than half atrial width (Fig. 11B)..... *arcuatus*  
Epigynal teeth separated by at least atrial width (Fig. 39A) ..... 46

46. Epigynal teeth situated laterad of atrium, away from atrial margins; copulatory ducts looped  
medially on spermathecae (Figs. 68A–B) ..... *wuermlii*  
Epigynal teeth situated near atrial margins; copulatory ducts looped anteriorly on spermathecae  
(Figs. 39A–B)..... *lutulentus*

47. Copulatory ducts looped around spermathecae (Figs. 19B; 51B) ..... 48  
Copulatory ducts not looped ..... 49

48. Copulatory ducts originating medially, with two loops around spermathecae (Fig. 51B)  
..... *potanini*  
Copulatory ducts originating laterally, with one loop (Fig. 19B) ..... *carinatus*

49. Spermathecal bases with diverticula (Fig. 48B) ..... *paraterebratus*  
Spermathecal bases without diverticula ..... 50

50. Spermathecal bases situated closed together. .... *pervicax*  
Spermathecal bases separated at least by their width (Fig. 55B) ..... 51

51. Epigynal hoods situated posteriorly near epigastric furrow; copulatory ducts large; spermathecal stalks broad, not convoluted (Figs. 55A–B) ..... *quadratus*  
Epigynal hoods situated anteriorly; copulatory ducts large; spermathecal stalks convoluted (Figs. 54A–B) ..... *pseudowuermlii*
52. Copulatory ducts originating mesad of spermathecae, extending laterad of spermathecae with 4–5 loops (Fig. 57B) ..... *rufulus*  
Copulatory ducts originating either mesad or laterad of spermathecae, not extending laterad of spermathecae and looped ..... 53
53. Copulatory ducts situated laterad of spermathecae (Fig. 31B) ..... 54  
Copulatory ducts situated mesad of spermathecae (Fig. 33B) ..... 56
54. Copulatory ducts only laterally extending, not anteriorly expanding; spermathecae anteriorly converging, not looped (Fig. 23B) ..... *griswoldi*  
Copulatory ducts expanding anteriorly; spermathecae looped (Fig. 23B) ..... 55
55. Atrium with distinct lateral margins; epigynal hoods situated near atrium; spermathecae looped laterally (Fig. 7A–B) ..... *absentis*  
Atrium with distinct anterior margin; epigynal hoods widely separated from atrium; spermathecae looped medially (Fig. 23A–B) ..... *curiosus*
56. Epigynal hoods situated laterally, laterad of atrium (Fig. 42A) ..... 57  
Epigynal hoods situated anteriorly, anterad of atrium (Fig. 27A) ..... 59
57. Copulatory ducts not looped (Fig. 63B) ..... *terebratus*  
Copulatory ducts looped around spermathecae (Fig. 42B) ..... 58
58. Copulatory ducts with two loops; spermathecae with distal end strongly convoluted (Fig. 42B) ..... *molluscus*  
Copulatory ducts with one loop; spermathecae with distal end smooth, not convoluted (Fig. 33B) ..... *haopingensis*
59. Spermathecae elongated, looped ..... 60  
Spermathecae short, not looped ..... 62
60. Spermathecal bases extending laterally, away from each other ..... *tryblionatus*  
Spermathecal bases extending medially, approaching each other ..... 61
61. Spermathecal stalks strongly convoluted, shaped like circles ..... *syzygiatus*  
Spermathecal stalks extending laterally, then converging medially, not shaped like circles ..... *streptus*
62. Copulatory ducts broad, strongly extending anteriorly (Fig. 41B) ..... *magniceps*  
Copulatory ducts small, not anteriorly extending ..... 63
63. Epigynum wrinkly anterad of atrium as in Figs. 27A; 47A ..... 64  
Epigynum not wrinkly ..... 67
64. Spermathecal bases broader than stalks (Fig. 47B) ..... 65  
Spermathecal bases narrower than stalks (Fig. 27B) ..... 66
65. Spermathecal heads situated anteriorly on spermathecae (Fig. 47B) ..... *parabrunneus*  
Spermathecal heads situated medially on spermathecae (Fig. 52B) ..... *pseudobrunneus*



66. Spermathecae with converging distal ends ..... *brunneus*  
Spermathecae with widely separated distal ends (Fig. 27B)..... *disgregus*

67. Spermathecae strongly expanded anteriorly; spermathecal heads situated medially on spermathecae (Fig. 62B) ..... *striolatus*  
Spermathecae not anteiorly expanded, or slightly expanded; spermathecal heads situated anteiorly on spermathecae (Fig. 18B)..... 68

68. Spermathecae medially lobed (Fig. 53B) ..... 69  
Spermathecae not lobed ..... 70

69. Spermathecae with lobes close together, slightly separated (Fig. 18B) ..... *capitulatus*  
Spermathecae with lobes separated at least by their sizes (Fig. 53B)..... *pseudocapitulatus*

70. Spermathecae widely separated at least by their sizes (Fig. 28B) ..... 71  
Spermathecae separated by less than their sizes (Fig. 29B)..... 72

71. Spermathecal heads and copulatory ducts distinct (Fig. 28B) ..... *dissitus*  
Spermathecal heads and copulatory ducts indistinct..... *amygdaliformis*

72. Spermathecal bases broader than stalks (Fig. 29B) ..... *dubius*  
Spermathecal bases narrower than stalks ..... 73

73. Copulatory ducts large, anteriorly extending; spermathecal heads extending mesad of spermathecae (Fig. 59B)..... *simplicidens*  
Copulatory ducts small, not anteriorly extending; spermathecal heads extending anterad of spermathecae (Fig. 49B) ..... *patellabifidus*

**Key To Males of the Species of the Genus *Draconarius***

1. Patellar apophysis absent (Fig. 13E) ..... 2  
Patellar apophysis present (Fig. 39E) ..... 12

2. Median apophysis not spoon-like (Figs. 19C-E) ..... 3  
Median apophysis spoon-like (Fig. 13D)..... 4

3. Median apophysis strongly bifurcate (Figs. 19C-E)..... *carinatus*  
Median apophysis elongated, not bifurcate..... *nudulus*

4. Conductor long, extending posteriorly, reaching embolic base (Figs. 17B; 57D) ..... 5  
Conductor short, retrolaterally or anteriorly extending (Figs. 13D; 44C)..... 6

5. Embolus broad, posterior in origin, (Figs. 57C, D) ..... *rufulus*  
Embolus slender, retrolateral in origin, (Figs. 17A-B)..... *bituberculatus*

6. Embolus prolateral in origin (Fig. 12A) ..... 7  
Embolus posterior in origin (Fig. 13D) ..... 8

7. Conductor with slender apex; median apophysis strongly elongated (Fig. 12)..... *argenteus*  
Conductor with broad apex; median apophysis slightly elongated (Fig. 20) .... *chaiqiaoensis*

8. Embolus broad, conductor broad, deeply grooved (Figs. 38A, 44C) ..... 9  
Embolus slender, conductor slender, slightly grooved (Figs. 13C-E) ..... 11

9. Embolus with narrow base; median apophysis not elongated (Figs. 38A–B) . . . . .	<i>linxiaensis</i>
Embolus with broad base, median apophysis strongly elongated (Fig. 44C) . . . . .	10
10. Embolus with slender apex . . . . .	<i>colubrinus</i>
Embolus with broad apex (Figs. 44C, D) . . . . .	<i>neixiangensis</i>
11. Conductor with dorsal edge slightly toothed, as in Figures 8–43:3–5 (Hu, 2001). . .	<i>altissimus</i>
Conductor not toothed (Figs. 13C–E) . . . . .	<i>aspinatus</i>
12. Patellar apophysis bifurcate (Fig. 49D) . . . . .	13
Patellar apophysis not bifurcate (Figs. 39D, E) . . . . .	16
13. Median apophysis spoon-like (Fig. 65B) . . . . .	<i>uncinatus</i>
Median apophysis not spoon-like (Figs. 49C, D) . . . . .	14
14. Conductor with distal part spiraled . . . . .	<i>tryblionatus</i>
Conductor not spiraled . . . . .	15
15. Embolic base notched. . . . .	<i>himalayaensis</i>
Embolic base not notched (Figs. 49C, D) . . . . .	<i>patellabifidus</i>
16. Median apophysis absent . . . . .	17
Median apophysis present . . . . .	18
17. Embolus broad (Fig. 23C) . . . . .	<i>curiosus</i>
Embolus slender (Fig. 7C) . . . . .	<i>absentis</i>
18. Median apophysis not spoon-like (Figs. 27C; 29C) . . . . .	19
Median apophysis spoon-like (Fig. 67D) . . . . .	21
19. Median apophysis broad; patellar apophysis strong curved (Figs. 27C, D) . . . . .	<i>disgregus</i>
Median apophysis slender; patellar apophysis not curved (Fig. 29C) . . . . .	20
20. Patellar apophysis as long as or longer than tibia (Figs. 29 C, D) . . . . .	<i>dubius</i>
Patellar apophysis much shorter than tibia (Figs. 35A–B) . . . . .	<i>incertus</i>
21. Conductor as long as cymbium, looping and extending posteriorly . . . . .	<i>syzygiatus</i>
Conductor short . . . . .	22
22. Embolic base lobed (Fig. 63D) . . . . .	<i>terebratus</i>
Embolic base not lobed . . . . .	23
23. Conductor strongly bifurcate (Figs. 16C; 46B) . . . . .	24
Conductor not bifurcate. . . . .	26
24. Conductor deeply bifurcate from the base (Fig. 16C) . . . . .	<i>calcariformis</i>
Conductor slightly bifurcate from the distal part (Fig. 46B) . . . . .	25
25. Embolus broad, cymbial furrow short (Figs. 46A–B) . . . . .	<i>ornatus</i>
Embolus slender, cymbial furrow long. . . . .	<i>huizhunesis</i>
26. Conductor with apex slightly spiraled, anteriorly extending (Figs. 26C–E) . . . .	<i>digitusiformis</i>
Conductor slender, retrolaterally extending (Fig. 67D) . . . . .	27

27. Patellar apophysis as long as tibia. . . . .	<i>funiushanensis</i>
Patellar apophysis short, less than tibial length . . . . .	28
28. Embolus prolateral in origin (Fig. 60D) . . . . .	29
Embolus posterior in origin (Fig. 67D). . . . .	30
29. RTA longer than half tibial length (Fig. 60E). . . . .	<i>singulatus</i>
RTA shorter than half tibial length . . . . .	<i>everesti</i>
30. RTA shorter than half tibial length (Figs. 39D, E) . . . . .	31
RTA longer than half tibial length (Figs. 22D, E). . . . .	32
31. Conductor long, looped posteriorly (Fig. 39D). . . . .	<i>lutulentus</i>
Conductor short, not looped (Fig. 67D). . . . .	<i>wudangensis</i>
32. Median apophysis not extending, with anterior edge not free (Figs. 22D; 50D). . . . .	33
Median apophysis extending, with anterior free edge (Figs. 10A; 31C) . . . . .	36
33. Cymbial furrow less than half cymbial length (Fig. 14C) . . . . .	34
Cymbial furrow at least half cymbial length (Fig. 22C). . . . .	35
34. Conductor with broad anterior edge (Fig. 64B). . . . .	<i>tibetensis</i>
Conductor without broad anterior edge (Fig. 14B). . . . .	<i>baronii</i>
35. Embolic base short, conductor positioned posteriorly (Fig. 50D). . . . .	<i>penicillatus</i>
Embolic base long, conductor positioned anteriorly (Fig. 22D) . . . . .	<i>coreanus</i>
36. Embolic base short . . . . .	<i>venustus</i>
Embolic base elongated (Fig. 31C). . . . .	37
37. Conductor with narrow dosal edge; embolic base with a small lobe on prolateral side . . . . .	<i>trifasciatus</i>
Conductor with broad dosal edge; embolic base normal, without lobe (Figs. 10A–B) . . . .	38
38. Embolus stout (Fig. 10A) . . . . .	<i>agrestis</i>
Embolus slender (Fig. 31C). . . . .	<i>griswoldi</i>

***Draconarius absentis* Wang, sp. nov.**

Figures 7A–D; Map 3

**TYPES.**— Male holotype and female paratype from Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, 2300m, Baoshan Prefecture, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI; 9 female and 7 male paratypes from Pass over Gaoligongshan at 2100 m, Nankang, 36 air km SE TengChong, 24°50'N, 98°47'E, native forest, Baoshan Prefecture, Yunnan, China (November 4–7, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (7 females and 5 males) and CAS (2 males and 2 females); 3 male and 5 female paratypes from Luoshuidong, Baoshan, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in CAS.

**ETYMOLOGY.**— The specific name refers to the absence of both epigynal teeth and median apophysis, which differs from most other *Draconarius*.

**DIAGNOSIS.**— This new species can be distinguished from other *Draconarius* by the absence

of epigynal teeth, the broad copulatory ducts, the short spermathecae of female (Figs. 7A–B), and by the short cymbial furrow, the trifid conductor, prolateral origin of embolus, and the absence of median apophysis of male (Figs. 7C–D).

**FEMALE.**— Total length 9.80. Carapace 4.60 long, 2.90 wide. Abdomen 5.20 long, 2.20 wide. Eye sizes and interdistances: AME 0.11, ALE 0.20, PME 0.18, PLE 0.20; AME-AME 0.10, AME-ALE 0.07, PME-PME 0.15, PME-PLE 0.20, AME-PME 0.17. Leg measurements: I: 12.0 (3.40, 4.10, 2.80, 1.80); II: 10.8 (3.00, 3.50, 2.60, 1.70); III: 9.76 (2.60, 3.16, 2.50, 1.50); IV: 13.2 (3.40, 4.30, 3.60, 1.90). Chelicerae with three promarginal and two retromarginal teeth. Epigynal teeth absent; atrium large, with broad anterior atrial margin; epigynal hoods deep, situated near anterior atrial margin; copulatory ducts broad, extending anteriorly and laterally; spermathecal heads large, situated laterad of spermathecae; spermathecal bases small, widely separated; spermathecal stalks separated, anteriorly extending and diverging (Figs. 7A–B).

**MALE.**— Total length 9.60. Carapace 4.80 long, 3.10 wide. Abdomen 4.80 long, 2.80 wide. Eye sizes and interdistances: AME 0.16, ALE 0.21, PME 0.19, PLE 0.20; AME-AME 0.08, AME-ALE 0.06, PME-PME 0.10, PME-PLE 0.19, AME-PME 0.16. Leg measurements: I: 14.3 (3.80, 4.86, 3.50, 2.10); II: 12.6 (3.40, 4.12, 3.10, 2.00); III: 10.6 (3.00, 3.60, 2.20, 1.76); IV: 15.4 (3.90, 4.80, 4.50, 2.20). Chelicerae with three promarginal and two retromarginal teeth. Male palp with patellar apophysis short; RTA long; lateral tibial apophysis large, near RTA; cymbial furrow short; conductor moderately long, with trifid apex; conductor dorsal apophysis present; conductor lamella small; embolus short, prolateral in origin; median apophysis absent (Figs. 7C–D).

**DISTRIBUTION.**— China (Yunnan) (Map 3).

**OTHER MATERIAL EXAMINED.**— None.

### ***Draconarius acidentatus* (Peng and Yin, 1998), NEW COMBINATION**

Figures 8A–B; 97A; Map 3

*Coelotes acidentatus* Peng and Yin, 1998:26, figs. 1–3 (female holotype and 1 female paratype from Huangsang, Suining, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:365.

**DIAGNOSIS.**— The female of this species can be easily recognized by the long, closely situated epigynal teeth, the deep, medially situated epigynal hoods, the laterally originating copulatory ducts, and the posteriorly situated spermathecal heads (Figs. 8A–B).

**DESCRIPTION.**— Described by Peng and Yin (1998). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth long, broad, originating anteriorly, situated close together; epigynal hoods deep, situated medially; atrium small, near epigastric furrow; copulatory ducts originating laterad of spermathecae, anteriorly extending; spermathecal heads long, originating posteriorly laterad of spermathecae; spermathecal bases broad, slightly separated; spermathecal stalks broad, close together (Figs. 8A–B). Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 3).

**MATERIAL EXAMINED.**— CHINA: Hunan: Suining, Huangsang, August 1996, female holotype (Yin, C.M. and X.J. Peng, HBI); Suining, Huangsang, May 28, 1996, 1 female paratype (Yin, C.M., X.J. Peng and Y.J. Zhang, HBI).

### ***Draconarius adligansu* (Peng and Yin, 1998), NEW COMBINATION**

Figures 9A–B; 97B; Map 3

*Coelotes adligansu* Peng and Yin, 1998: 26, figs. 4–6 (female holotype from Nanyue, Hunan, China, in HBI, examined).

**DIAGNOSIS.**— The female of this species is similar to *D. denisi* in having the anteriorly expanding copulatory ducts but can be distinguished by the posteriorly situated, moderately separated epigynal teeth (situated near atrium, separated by less than atrial width) and the anteriorly expanded spermathecae (Figs. 9A–B).

**DESCRIPTION.**— Described by Peng and Yin (1998). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated on anterior atrial margin, separated by less than atrial width; atrium with distinct median carina; copulatory ducts large, anteriorly extending; spermathecal heads small, anteriorly situated; spermathecal bases small, widely separated; spermathecal stalks short, anteriorly expanding and slightly diverging (Figs. 9A–B). Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 3).

**MATERIAL EXAMINED.**— CHINA: Hunan: Nanyue, August 3–7, 1995, female holotype (C.M. Yin, HBI).

***Draconarius agrestis* Wang, sp. nov.**

Figures 10A–B; Map 4

**TYPES.**— Male holotype and 2 male paratypes from from Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, 2300m, Baoshan Prefecture, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (holotype male and 1 male paratype) and CAS (1 male paratype).

**ETYMOLOGY.**— The specific name refers to the large cymbial furrow and long, broad embolus.

**DIAGNOSIS.**— The male of this new species is similar to *D. griswoldi* in having a small patellar apophysis, an elongated cymbial furrow, and a posteriorly originated, long embolus but can be distinguished by the broad embolus, the broad conductor apex, and the spoon-like median apophysis (Figs. 10A–B).

**MALE.**— Total length 9.60. Carapace 4.80 long, 3.40 wide. Abdomen 4.80 long, 4.00 wide. Eye sizes and interdistances: AME 0.16, ALE 0.20, PME 0.21, PLE 0.21; AME-AME 0.09, AME-ALE 0.05, PME-PME 0.09, PME-PLE 0.24, AME-PME 0.11. Leg measurements: I: 13.7 (3.92, 4.60, 3.20, 1.94); II: 12.1 (3.40, 3.92, 2.80, 1.80); III: 8.18 (2.60, 1.92, 2.36, 1.30); IV: 12.4 (3.50, 4.24, 3.20, 1.50). Chelicerae with three promarginal and two retromarginal teeth. Male palp with small patellar apophysis; RTA long; lateral tibial apophysis small, widely separated with RTA; cymbial furrow large, longer than half cymbial length; conductor broad, with broad, membranous dorsal edge and large basal lamella; conductor dorsal apophysis present; embolus posterior in origin, long, broad; median apophysis spoon-like, elongated (Figs. 10A–B).

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 4).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius altissimus* (Hu, 2001), NEW COMBINATION**

Map 3

*Coeolotes altissimus* Hu, 2001:131, figs. 8–43:1–5 (female holotype and male paratype from GongbuJiangda, Tibet, China, in SDU, not examined).

**DIAGNOSIS.**— The male of this species is similar to *D. aspinatus* and can only be distinguished

by the slightly toothed conductor. The female is similar to *D. himalayaensis* and *D. subtitanus* in having the short epigynal teeth, anteriorly situated spermathecal heads and rounded, closely situated spermathecae but can be distinguished from *D. himalayaensis* by the epigynal teeth position (situated close to atrium), from *D. subtitanus* by the non separated spermathecae.

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, widely separated, situated near anterior atrium; atrium small, posteriorly situated; spermathecal heads situated anteriorly; spermathecal bases widely separated; spermathecal stalks broad, rounded, close together. Male palp without patellar apophysis; RTA long; lateral tibial apophysis small; cymbial furrow large, longer than half cymbial length; conductor slender; embolus long, posterior in origin; median apophysis spoon-like, elongated.

**DISTRIBUTION.**— China (Tibet) (Map 3).

**MATERIAL EXAMINED.**— None.

***Draconarius amygdaliformis* (Zhu and Wang, 1991), NEW COMBINATION**

Map 4

*Coelotes amygdaliformis* Zhu and Wang, 1991:2, figs. 8–9 (female holotype, 2 female paratypes from Xishan, Kunming, Yunnan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:365, figs. 216H–I.

**DIAGNOSIS.**— The female of this species is similar to *Tegenaria domestica* by having small, posteriorly situated atrium and small, widely separately spermathecae.

**DESCRIPTION.**— See Zhu and Wang (1991). Chelicerae with three promarginal and two retromarginal teeth. Female without epigynal teeth; atrium small, posteriorly situated, near epigastric furrow; spermathecae small, rounded, widely separated. Male unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 4).

**MATERIAL EXAMINED.**— None.

***Draconarius arcuatus* (Chen, 1984)**

Figures 11A–B; Map 4

*Coelotes arcuatus* Chen, 1984:2, figs. 3–4 (4 female paratypes from Huanglongdong, Hangzhou, Zhejiang, China, in HTC, examined).— Chen and Zhang, 1991:189, figs. 187.1–2;— Song, Zhu and Chen, 1999:374, figs. 216J–K, 218A–B.

*Draconarius arcuatus*: Wang, 2002:66.

**DIAGNOSIS.**— The female of this species is similar to *D. cheni* in having a broad, medially situated, anteriorly expanding copulatory ducts but can be distinguished by the broad atrium (twice epigynal teeth distance) and the distinct, anteriorly situated spermathecal heads (Figs. 11A–B).

**DESCRIPTION.**— The female was described by Chen (1984). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth situated posteriorly near atrium, close together; atrium slightly extending posteriorly; copulatory ducts originating posteriorly, extending anteriorly, slightly spiraled; spermathecal heads distinct, anteriorly situated; spermathecal bases small, widely separated; spermathecal stalks long, laterally extending (Figs. 11A–B). Male unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 4).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang**: Hangzhou, Huanglongdong, February 26 to March 1, 1982, 4 female paratypes (Z. F. Chen, HTC).

***Draconarius argenteus* (Wang et al., 1990), NEW COMBINATION**

Figures 12A–B; Map 4

*Coelotes argenteus* Wang et al., 1990:229, figs. 117–119 (male holotype from Jinhong, Yunnan, China, in HBI, examined). — Song, Zhu and Chen, 1999:374, figs. 218C, J.

**DIAGNOSIS.**— The male is similar to *D. nudulus* in lacking a patellar apophysis and having a short conductor but can be distinguished by the short RTA (half tibial length), the spoon-like median apophysis, and the lobed embolic base (Figs. 12A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Chelicerae with three promarginal and five retromarginal teeth. Male palp without patellar apophysis; RTA approximately half tibial length; lateral tibial apophysis large, situated anteriorly and near RTA; cymbial furrow slightly less than half cymbial length; conductor broad, with slender apex; conductor dorsal apophysis present; conductor lamella broad; embolus prolateral in origin; embolic base with a lobe on its retrolateral side; median apophysis spoon-like, strongly elongated (Figs. 12A–B). Female unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 4).

**MATERIAL EXAMINED.** — CHINA: **Yunnan:** Jinhong, October 21, 1987, male holotype (J.F. Wang, HBI).

***Draconarius aspinatus* (Wang et al., 1990)**

Figures 13A–E; Map 5

*Coelotes aspinatus* Wang et al., 1990:207, figs. 68–72 (female holotype and male paratype from Huangshan, Anhui, China, in HBI, examined). — Song, Zhu and Chen, 1999:374, figs. 216L–M, 218D, K.

*Draconarius aspinatus:* Wang, 2002:66.

**DIAGNOSIS.**— The male of this species is similar to *D. altissimus* and can only be recognized by non-toothed conductor. The female is similar to *D. wudangensis* in having the medially situated and widely separated epigynal teeth, and similar spermathecal tubes but can be distinguished by the epigynal teeth position (separated by less than atrial width) (Figs. 13C–E).

**DESCRIPTION.**— Described by Wang et al. (1990). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated anterad of atrium; atrium small, slightly expanded posteriorly; copulatory ducts posteriorly originating, extending mesad of spermathecae; spermathecal heads slender, situated medially on spermathecae; spermathecal bases small, widely separated; spermathecal stalks broad, anteriorly expanded and converging (Figs. 13A–B). Male palp without patellar apophysis; RTA long; lateral tibial apophysis small; cymbial furrow large, longer than half cymbial length; conductor slender, with large basal lamella; conductor dorsal apophysis present; embolus posterior in origin; median apophysis spoon-like, elongated (Figs. 13C–E).

**DISTRIBUTION.**— China (Anhui) (Map 5).

**MATERIAL EXAMINED.**— CHINA: **Anhui:** Huangshan, female holotype and male paratype, October 24, 1974 (J.F. Wang and C.M. Yin, HBI).

***Draconarius baronii* (Brignoli, 1978)**

Figures 14A–C; Map 5

*Coelotes baronii* Brignoli, 1978:42, figs. 17–18 (male holotype from Dorjula, Bhutan, in NHMB, examined) (male only, female paratype is *Himalcoelotes brignolii* Wang, 2002).

*Draconarius baronii:* Wang, 2002:66

**DIAGNOSIS.**— The male of this species is similar to *D. tibetensis* but can be distinguished by the long, slender conductor (Figs. 14A–C).

**DESCRIPTION.**— Described by Brignoli (1978). Chelicerae with three promarginal and two retromarginal teeth. Male palp with patellar apophysis short; RTA long; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor long, slender, with large basal lamella; conductor dorsal apophysis present; embolus posterior in origin; median apophysis spoon-like, elongated (Figs. 14A–C). Female unknown.

**DISTRIBUTION.**— Bhutan (Map 5).

**MATERIAL EXAMINED.**— BHUTAN: **Dorjula:** 3100 m, June 6, 1972, male holotype (NHMB, 2302a, 2302b) (female paratype is *Himalcoelotes brignolii* Wang, 2002).

***Draconarius baxiantaiensis* Wang, sp. nov.**

Figures 15A–B; 97C; Map 5

**TYPES.**— Female holotype and female paratype from Baxiantai, Taibai Mt, Shaanxi, China (July 13, 1991; X.P. Wang), deposited in IZB.

**ETYMOLOGY.**— The specific name refers to the type locality.

**DIAGNOSIS.**— The female of this new species is similar to *D. potanini* in having looped copulatory ducts and broad, long spermathecae but can be distinguished by the dorsally originating spermathecal heads and the relatively short copulatory ducts (with only one loop) (Figs. 15A–B).

**FEMALE.**— Total length 8.18. Carapace 4.01 long, 2.65 wide. Abdomen 4.17 long, 2.72 wide. Eye sizes and interdistances: AME 0.07, ALE 0.16, PME 0.12, PLE 0.15; AME–AME 0.1, AME–ALE 0.08, PME–PME 0.16, PME–PLE 0.19. Leg measurements: I: 8.92 (2.60, 3.22, 1.92, 1.18); II: 8.41 (2.43, 2.95, 1.88, 1.15); III: 7.85 (2.22, 2.82, 1.71, 1.10); IV: 10.8 (2.87, 3.45, 2.97, 1.47). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated posteriorly near atrium; atrium small, posteriorly situated; copulatory ducts originating posteriorly mesad of spermathecae, extending laterally and formed one loop around spermathecae; spermathecal heads long, slender, originating from dorsal side of spermathecae; spermathecal bases small, widely separated; spermathecal stalks broad, anteriorly extending, slightly converging (Figs. 15A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Shaanxi) (Map 5).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius bituberculatus* (Wang et al., 1990), NEW COMBINATION**

Figures 16A–C; Map 6

*Coelotes bituberculatus* Wang et al., 1990:209, figs. 73–75 (male holotype from Huangshan, Anhui, China, in HBI, examined).— Song, Zhu and Chen, 1999:374, figs. 218F, M.

**DIAGNOSIS.**— The male of this species can be easily distinguished from other *Draconarius* by the absence of a patellar apophysis, the broad, posteriorly extending conductor (reaching embolic base), and the retrolaterally extending embolic base (Figs. 16A–C).

**DESCRIPTION.**— Described by Wang et al. (1990). Chelicerae with three promarginal and two retromarginal teeth. Male palp without patellar apophysis; RTA long, strongly elevated from tibia; lateral tibial apophysis present; cymbial furrow slightly longer than half cymbium length; conductor long, broad, posteriorly extending and reaching embolic base, with small basal lamella; conduc-



tor dorsal apophysis short; embolus long, retrolateral in origin; median apophysis spoon-like, elongated (Figs. 16A–C). Female unknown.

**DISTRIBUTION.**— China (Anhui) (Map. 6).

**MATERIAL EXAMINED:** CHINA: **Anhui:** Huangshan, October 27, 1974, female holotype (C. M. Yin and J. F. Wang, HBI).

***Draconarius brunneus* (Hu and Li, 1987), NEW COMBINATION**

Map 5

*Coelotes brunneus* Hu and Li, 1987:277, figs. 1–2 (female holotype and female paratype from Yadong, Tibet, China, in SDU, not examined).— Song, Zhu and Chen, 1999:374, figs. 216V–W;— Hu, 2001:136, figs. 8–46:1–2.

**DIAGNOSIS** – The female of this species is similar to *D. disgregus* in lacking epigynal teeth and having broad spermathecae but can be distinguished by the non-convoluted, anteriorly converging spermathecae.

**DESCRIPTION.**— See Hu and Li (1987). Chelicerae with three promarginal and two retromarginal teeth. Female without epigynal teeth; spermathecal bases widely separated; spermathecal stalks broad, anteriorly converging. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 5).

**MATERIAL EXAMINED.**— None.

***Draconarius calcariformis* (Wang, 1994)**

Figures 17A–D; 97D; Map 6

*Coelotes calcariformis* Wang, 1994:287, figs. 6–10 (1 male and 1 female types, no holotype indicated, from Dabashan, Hubei, China, in HBI, examined).— Song, Zhu and Chen, 1999:374, figs. 217A–B, 218H–I. *Draconarius calcariformis*: Wang, 2002:67.

**DIAGNOSIS.**— The female is similar to *D. colubrinus* and *D. davidi* in having the posteriorly situated atrium, anteriorly and closely situated epigynal teeth, and similar spermathecal tubes but can be distinguished by the broad, slightly bifurcate anterior atrial margin and the strongly convoluted spermathecae (Figs. 17A–B). The male can be easily identified by the strongly bifurcate conductor and the ventrally and laterally concave tibia (Figs. 17C–D).

**DESCRIPTION.**— Described by Wang (1994). Chelicerae with three promarginal and two retromarginal teeth. Epigynal teeth short, anteriorly situated, adjacent; atrium broad, situated posteriorly near epigastric furrow; anterior atrial margin broad, slightly bifurcate; copulatory ducts originating posteriorly, extending mesad of spermathecae; spermathecal heads slender, situated medially on spermathecae; spermathecal bases small, widely separated; spermathecal stalks anteriorly expanded and converging (Figs. 17A–B). Male palp with a short, blunt patellar apophysis; tibia concave ventrally and laterally; RTA long, almost as long as tibia; lateral tibial apophysis small, situated anteriorly near RTA; cymbial furrow short; conductor strongly bifurcate, with small basal lamella; conductor dorsal apophysis present; embolus posterior in origin; median apophysis spoon-like, small, slightly elongated (Figs. 17C–D).

**DISTRIBUTION.**— China (Hubei) (Map 6).

**MATERIAL EXAMINED.**— CHINA: **Hubei:** Dabashan, Nov. 10, 1990, 1 male and 1 female types (J.F. Wang, HBI).

***Draconarius capitulatus* Wang, sp. nov.**

Figures 18A–B; Map 6

**TYPES.**— Female holotype and 5 female paratypes from Pianma Yakou, pass over Gaoligongshan, at elev. 3200m, 25°58'N, 98°41'E, Nujiang Prefecture, Yunnan, China (October 11, 1998; C. Griswold, D. Kavanaugh, C.-L. Long), deposited in HBI (male holotype and 3 female paratypes) and CAS (2 female paratypes); 1 female paratype from Nujiang Prefecture, Nujiang State Nature Reserve, No. 12 Bridge Camp area, 16.3 air km W of Gongshan, N27.715°/E98.502°, 2775m, Gaoligong Shan, Yunnan, China (July 15–19, 2000; H.M. Yan, D. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong), deposited in CAS.

**ETYMOLOGY.**— The specific name refers to the prominent spermathecal heads.

**DIAGNOSIS.**— The female of this species is similar to *D. pseudocapitulatus* in lacking epigynal teeth and having short, medially lobed spermathecae but can be distinguished by the closely situated, not anteriorly expanded spermathecae (Figs. 18A–B).

**FEMALE.**— Total length 10.6. Carapace 5.20 long, 3.60 wide. Abdomen 5.40 long, 3.60 wide. Eye sizes and interdistances: AME 0.16, ALE 0.27, PME 0.25, PLE 0.25; AME-AME 0.12, AME-ALE 0.10, PME-PME 0.15, PME-PLE 0.28, AME-PME 0.20. Leg measurements: I: 13.1 (3.80, 4.70, 3.04, 1.60); II: 12.3 (3.60, 4.42, 2.80, 1.50); III: 10.3 (2.80, 3.60, 2.60, 1.30); IV: 14.3 (4.00, 4.80, 3.80, 1.70). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth absent; atrium posteriorly situated; copulatory ducts originating posteriorly, extending mesad of spermathecae, slightly separated; spermathecal heads large, situated anteriorly on inner side of spermathecae; spermathecal bases small, widely separated; spermathecal stalks short, broad (Figs. 18A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 6).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius carinatus* (Wang et al., 1990), NEW COMBINATION**

Figures 19A–E; Map 7

*Coelotes carinatus* Wang et al., 1990:211, figs. 76–80 (female holotype, male and female paratypes from Huangshan, Anhui, China, in HBI, examined).— Song, Zhu and Chen, 1999:374, figs. 217C–D, 219A–H.

**DIAGNOSIS.**— This species can be easily distinguished from other coelotines by the broad, laterally originating, medially extending copulatory ducts of female (Figs. 19A–B), and by the absence of patellar apophysis, the strongly bifurcate median apophysis, and the broad embolus of male (Figs. 19C–E).

**DESCRIPTION.**— Described by Wang et al. (1990). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth large, situated posteriorly on anterior atrial margin; atrium small, posteriorly situated; copulatory ducts originating laterally, looped around spermathecae and extending medially; spermathecal heads small, anteriorly situated; spermathecae small, widely separated (Figs. 19A–B). Male palp lacking patellar apophysis; RTA strongly elevated from tibia; lateral tibial apophysis widely separated from RTA; cymbial furrow short; conductor broad, deeply grooved, with small basal lamella; conductor dorsal apophysis present; embolus broad, posterior in origin; median apophysis strongly bifurcate, not spoon-like (Figs. 19C–E).

**DISTRIBUTION.**— China (Anhui) (Map 7).

**MATERIAL EXAMINED.**— CHINA: Anhui: Huangshan, October 27, 1974, female holotype, 1 male and 1 female paratypes (C.M. Yin and J.F. Wang, HBI).

***Draconarius chaiqiaoensis* (Zhang, Peng and Kim, 1997), NEW COMBINATION**

Figures 20A–C; 97E; Map 6

*Coelotes chaiqiaoensis* Zhang, Peng and Kim, 1997:291, figs. 1–3 (male holotype from Chaiqiao, Ningbo, Zhejiang, China, in HBI, examined).

**DIAGNOSIS.**— The male of this species can be easily distinguished from other coelotines by the absence of a patellar apophysis, the short cymbial furrow, and the presence of short, broad conductor (Figs. 20A–C).

**DESCRIPTION.**— Described by Zhang, Peng and Kim (1997). Chelicerae with three promarginal and two retromarginal teeth. Male palp without patellar apophysis; RTA short, approximately half tibial length; lateral tibial apophysis widely separated from RTA; cymbial furrow short; conductor short, broad, with large dorsal edge and reduced basal lamella; conductor dorsal apophysis present; embolus prolateral in origin; median apophysis spoon-like, slightly elongated (Figs. 20A–C). Female unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 6).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang:** Ningbo, Chaiqiao, November 20, 1991, female holotype (Y.J. Zhang, HBI).

***Draconarius cheni* (Platnick, 1989)**

Figures 21A–B; Map 7

*Coelotes saxatilis* Chen, 1984:2, figs. 5–6 (female holotype and female paratype from Huanglongdong, Hangzhou, Zhejiang, China, in HTC, examined).— Chen and Zhang, 1991:189, figs. 188.1–2. (specific name preoccupied by Balckwall, 1833).

*Coelotes cheni* Platnick, 1989:422 (replacement name).— Song, Zhu and Chen, 1999:374, figs. 217E–F.

*Draconarius cheni*: Wang, 2002:67.

**DIAGNOSIS.**— The female of this species is similar to *D. arcuatus* in having a broad, medially situated copulatory ducts but can be distinguished by the small atrium (same width as epigynal teeth distance) and the indistinct spermathecal heads (Figs. 21A–B).

**DESCRIPTION.**— The female was described by Chen (1984). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated anterad of atrium, separated by atrial width; atrium small; copulatory ducts broad, originating posteriorly, extending anteriorly mesad of spermathecae, slightly folded; spermathecal heads not visible from dorsal view; spermathecal bases widely separated; spermathecal stalks long, slender, extending laterally and then slightly converging anteriorly (Figs. 21A–B). Male unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 7).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang:** Hangzhou, March 1977, female holotype and 1 female paratype (Z.F. Chen, HTC).

***Draconarius colubrinus* Zhang, Zhu and Song, 2002**

Map 7

*Draconarius colubrinus* Zhang, Zhu and Song, 2002:52, figs. 1–4 (male holotype and three female paratypes from Muyu, Shennongjia, Hubei, China, in HU, not examined).

**DIAGNOSIS.**— The female is similar to *D. calcariformis* in having the posteriorly situated atrium, anteriorly and closely situated epigynal teeth, and similar spermathecal tubes, but can be dis-

tinguished by the broad, moderately separated spermathecal bases. The male is similar to *D. neixiangensis* but can be recognized by the slender embolic apex.

**DESCRIPTION.**— See Zhang, Zhu and Song (2002). Cheliceral promargin with three teeth, retromargin with two. Epigynal teeth short, anteriorly situated, close together; atrium small, posteriorly situated, near epigastric furrow; copulatory ducts originating posteriorly, extending mesad of spermathecae; spermathecal heads situated laterally on spermathecae; spermathecal bases small, widely separated; spermathecal stalks broad, anteriorly expanded and converging. Male palp without patellar apophysis; RTA long; lateral tibial apophysis large; cymbial furrow short; conductor broad, with basal lamella small; conductor dorsal apophysis small; embolus broad, posterior in origin, with slender apex; median apophysis spoon-like, elongated.

**DISTRIBUTION.**— China (Hubei) (Map. 7).

**MATERIAL EXAMINED.**— None.

***Draconarius coreanus* (Paik and Yaginuma, 1969)**

Figures 22A–E; Map 7

*Coelotes coreanus* Paik and Yaginuma, 1969:837, figs. 62–64 (types deposited in the National Science Museum, Tokyo, not examined).— Paik, 1978:337, figs. 149.1–3.

*Draconarius coreanus*: Wang, 2002:67.

**DIAGNOSIS.**— The female is similar to *D. wudangensis* in having the medially situated and widely separated epigynal teeth, and similar spermathecal tubes but can be distinguished by the broad atrium and the slender spermathecal bases (Figs. 22A–B). The male is similar to *D. wudangensis* but can be recognized by the long RTA (more than half tibial length) and the broad median apophysis (Figs. 22C–E).

**DESCRIPTION.**— See Paik, Yaginuma and Namkung (1969). Cheliceral promargin with three teeth, retromargin with two. Epigynal teeth short, widely separated; atrium small, situated posteriorly near epigastric furrow; anterior atrial margin broad, membranous; copulatory ducts originating posteriorly near epigastric furrow, extending mesad of spermathecae; spermathecal heads situated medially on spermathecae; spermathecal bases small; spermathecal stalks broad, anteriorly expanded and converging (Figs. 22A–B). Male palp with patellar apophysis long; RTA long; lateral tibial apophysis present; cymbial furrow more than half cymbial length; conductor short, slender, with large basal lamella; conductor dorsal apophysis slender; embolus posterior in origin; median apophysis spoon-like, slightly elongated (Figs. 22C–E).

**DISTRIBUTION.**— South Korea (Map. 7).

**MATERIAL EXAMINED.**— SOUTH KOREA: Mt. Kwan-ak, May 5, 1991, 1 female (Cheol-hoe Jung, KAI); Mt. Hallason, August 7, 1984, 1 male (J.P. Kim, KAI).

***Draconarius curiosus* Wang, sp. nov.**

Figures 23A–D; Map 7

**TYPES.**— Male holotype and female paratype from Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, 2300m, Baoshan Prefecture, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI; 1 female paratype from Pass over Gaoligongshan at 2100 m. Nankang, 36 air km SE TengChong, 24°50'N, 98°47'E, native forest, Baoshan Prefecture, Yunnan, China (November 4–7, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI; 2 male and 15 female paratypes from Luoshuidong, Baoshan, Yunnan,

China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (1 male and 7 females) and CAS (1 male and 8 females).

**ETYMOLOGY.**— The specific name refers to its odd palpal structure.

**DIAGNOSIS.**— The female of this new species is similar to *D. griswoldi* by the absence of epigynal teeth and the laterally situated copulatory ducts but can be distinguished by the looped spermathecae (Fig. 23B). The male of this species can be easily recognized from all other coelotines by the absence of a median apophysis, the broad embolus, and strongly expanded embolic apex (Figs. 23C, D).

**FEMALE.**— Total length 6.80. Carapace 3.20 long, 2.14 wide. Abdomen 3.60 long, 2.50 wide. Eye sizes and interdistances: AME 0.09, ALE 0.19, PME 0.19, PLE 0.19; AME-AME 0.09, AME-ALE 0.04, PME-PME 0.08, PME-PLE 0.12, AME-PME 0.11. Leg measurements: I: 7.06 (2.12, 2.46, 1.60, 0.88); II: 6.44 (1.92, 2.18, 1.40, 0.94); III: 6.06 (1.64, 2.00, 1.52, 0.90); IV: 8.48 (2.20, 2.80, 2.34, 1.14). Chelicerae with three promarginal and two retromarginal teeth. Epigynal teeth absent; atrium broad; copulatory ducts broad, originating posteriorly, extending laterad of spermathecae, anteriorly converging; spermathecal heads situated inside spermathecal loops; spermathecal bases large, widely separated; spermathecal stalks extending with one loop (Figs. 23A–B).

**MALE.**— Total length 5.62. Carapace 2.90 long, 2.00 wide. Abdomen 2.72 long, 1.60 wide. Eye sizes and interdistances: AME 0.09, ALE 0.16, PME 0.18, PLE 0.18; AME-AME 0.05, AME-ALE 0.03, PME-PME 0.06, PME-PLE 0.07, AME-PME 0.09. Leg measurements: I: 7.82 (2.22, 2.74, 1.80, 1.06); II: 7.10 (2.04, 2.40, 1.66, 1.00); III: 6.46 (1.82, 2.02, 1.72, 0.90); IV: 8.72 (2.34, 2.68, 2.52, 1.18). Chelicerae with three promarginal and two retromarginal teeth. Male palp with patellar apophysis present; RTA long; lateral tibial apophysis small; cymbial furrow short; conductor short, deeply grooved, with basal lamella small; conductor dorsal apophysis small; embolus posterior in origin, broad, with strongly expanded apex; median apophysis absent (Figs. 23C, D).

**DISTRIBUTION.**— China (Yunnan) (Map 7).

**OTHER MATERIAL EXAMINED.**— None.

### *Draconarius davidi* (Schenkel, 1963)

Figures 24A–B; Map 8

*Coelotes davidi* Schenkel, 1963:283, fig. 159 (female holotype from Inkiaphou, Shensi, China, in MNHN, examined).— Song, Zhu and Chen, 1999:374.

*Draconarius davidi*: Wang, 2002:67.

**DIAGNOSIS.**— The female is similar to *D. calcariformis* in having the posteriorly situated atrium, anteriorly and closely situated epigynal teeth, and similar spermathecal tubes but can be distinguished by the broad spermathecal bases (Figs. 24A–B).

**DESCRIPTION.**— See Schenkel (1963). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, anteriorly situated, close together; atrium small, posteriorly situated, near epigastric furrow; copulatory ducts originating posteriorly, extending mesad of spermathecae; spermathecal heads not visible on the examined specimen; spermathecal bases small, widely separated; spermathecal stalks broad, anteriorly expanded and converging (Figs. 24A–B). Male unknown.

**DISTRIBUTION.**— China (Shaanxi) (Map 8).

**MATERIAL EXAMINED.**— CHINA: **Shaanxi** (Shensi): Inkiaphou, 1 female type, collected in 1873 (A. David, MNHN, B2011 bis.).

***Draconarius denisi* (Schenkel, 1963) NEW COMBINATION**

Figures 25A–B; Map 8

*Coelotes denisi* Schenkel, 1963:285, fig. 160 (female holotype from Lo Thoei-Tong, Yunnan, China, in MNHN, examined).

**DIAGNOSIS.**— The female of this species is similar to *D. adligansus* but can be separated by the anteriorly situated, widely separated epigynal teeth (away from atrium, separated by at least atrial width) and the small spermathecae (Figs. 25A–B).

**DESCRIPTION.**— See Schenkel (1963). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated anteriorly, widely separated; atrium small; copulatory ducts large, anteriorly extending, close together; spermathecal heads situated laterally; spermathecae short, widely separated (Figs. 25A–B). Male unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 8).

**MATERIAL EXAMINED.**— **CHINA:** Lo Thoei Tong (Yunnan?), March 2, 1925, female holotype (MNHN, B2011 bis).

***Draconarius digitusiformis* (Wang et al., 1990), NEW COMBINATION**

Figures 26A–E; 97F; Map 8

*Coelotes digitusiformis* Wang et al., 1990:205, figs. 63–67 (1 male and 2 female types, holotype not indicated, from Zhong Village, Ling County, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999: 374, figs. 217K–L, 219F, M.

*Coelotes shuangpaiensis* Peng, Gong and Kim, 1996:20, figs. 15–18 (male holotype from Shuangpai, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:378, figs. 226U, 228C. NEW SYNONYMY.

**DIAGNOSIS.**— This species can be easily distinguished by the closely situated epigynal teeth, the anteriorly situated, strongly convoluted copulatory ducts of female (Figs. 26A–B), and by the broad, anteriorly extending, slightly spiraled conductor of male (Figs. 26C–E).

**DESCRIPTION.**— Described by Wang et al. (1990). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth situated anteriorly, close together; atria small, widely separated; copulatory ducts broad, strongly convoluted, extending anterad of spermathecae; spermathecal heads situated posterad of copulatory ducts; spermathecal bases broad, close together; spermathecal stalks short, broad, extending laterally (Figs. 26A–B). Male palp with patellar apophysis long, broad; RTA almost as long as tibia; lateral tibial apophysis small; cymbial furrow more than half cymbial length; conductor short, broad, form broad groove and slightly spiraled apex, with large basal lamella; conductor dorsal apophysis small; embolus posterior in origin; median apophysis small, spoon-like (Figs. 26C–E).

**DISTRIBUTION.**— China (Hunan) (Map 8).

**MATERIAL EXAMINED.**— **CHINA:** **Hunan:** Ling County, Zhong Village, December 15, 1982, 1 male and 2 female types (J.F. Wang, HBI); Shuangpai, October 3, 1993, male holotype of *Coelotes shuangpaiensis* (C.L. He, HBI).

***Draconarius disgregus* Wang, sp. nov.**

Figures 27A–D; Map 8

**TYPES.**— Male holotype and female paratype from native forest in Gaoligongshan at 9.5 road km ESE Pianma, 25°59'N, 98°40'E, el. 2500m, Nujiang Prefecture, Yunnan, China (October 15–18, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI; 2 male and 5 female

paratypes from native forest in Gaoligongshan at 9.5 road km ESE Pianma, 25°59'N, 98°40'E, el. 2500m, Nujiang Prefecture, Yunnan, China (October 15–18, 1998; C. Griswold, D. Kavanaugh, C.-L. Long), deposited in HBI (1 male and 2 females) and CAS (1 male and 3 females).

**ETYMOLOGY.**— The specific name refers to its difference from other *Draconarius* in both male and female genitalia.

**DIAGNOSIS.**— The female of this species is similar to *D. brunneus* in lacking epigynal teeth and having broad spermathecae but can be distinguished by the convoluted, anteriorly diverging spermathecae. (Figs. 27A–B). The males can be easily distinguished from other coelotines by the short, slightly curved patellar apophysis and the broad, not spoon-like median apophysis (Figs. 27C–D).

**FEMALE.**— Total length 11.4. Carapace 5.80 long, 3.70 wide. Abdomen 5.60 long, 4.00 wide. Eye sizes and interdistances: AME 0.17, ALE 0.26, PME 0.24, PLE 0.25; AME-AME 0.15, AME-ALE 0.12, PME-PME 0.15, PME-PLE 0.25, AME-PME 0.20. Leg measurements: I: 13.8 (4.00, 4.80, 3.10, 1.90); II: 12.4 (3.60, 4.20, 2.80, 1.80); III: 10.9 (3.00, 3.60, 2.80, 1.50); IV: 14.7 (4.00, 4.80, 4.00, 1.90). Chelicerae with three promarginal and two retromarginal teeth. Epigynum lacking epigynal teeth; atrium small; copulatory ducts short, invisible from dorsal view; spermathecal heads large, anteriorly situated; spermathecal bases widely separated; spermathecal stalks broad, anteriorly extending and slightly converging (Figs. 27A–B).

**MALE.**— Total length 9.90. Carapace 5.10 long, 3.80 wide. Abdomen 4.80 long, 3.40 wide. Eye sizes and interdistances: AME 0.17, ALE 0.24, PME 0.21, PLE 0.23; AME-AME 0.10, AME-ALE 0.05, PME-PME 0.11, PME-PLE 0.19, AME-PME 0.20. Leg measurements: I: 17.3 (4.60, 5.90, 4.40, 2.40); II: 15.7 (4.20, 5.10, 4.10, 2.30); III: 13.4 (3.60, 4.20, 3.70, 1.90); IV: 17.1 (4.60, 5.20, 5.00, 2.30). Chelicerae with three promarginal and two retromarginal teeth. Male palp with patellar apophysis short, slightly curved dorsally; RTA almost as long as tibia; lateral tibial apophysis small; cymbial furrow short; conductor with broad apex and small basal lamella; conductor dorsal apophysis small; embolus prolateral in origin; median apophysis broad, membranous, not spoon-like (Figs. 27C–D).

**DISTRIBUTION.**— China (Yunnan) (Map 8).

**OTHER MATERIAL EXAMINED.**— None.

### *Draconarius dissitus* Wang, sp. nov.

Figures 28A–B; Map 9

**TYPES.**— Female holotype, 3 female paratypes from Yupin area (S. Tibet), Tibet, China (May, 1998; G. Schaller), deposited in AMNH.

**ETYMOLOGY.**— The specific name refers to the widely separated spermathecae.

**DIAGNOSIS.**— The female of this species is similar to *D. capitulatus* and *D. pseudocapitulatus* but can be distinguished by the absence of medially expanded spermathecal lobes and the presence of small, widely separated spermathecae (Figs. 28A–B).

**FEMALE.**— Total length 13.8. Carapace 5.80 long, 4.00 wide. Abdomen 8.00 long, 5.20 wide. Eye sizes and interdistances: AME 0.18, ALE 0.26, PME 0.22, PLE 0.24; AME-AME 0.12, AME-ALE 0.10, PME-PME 0.22, PME-PLE 0.25, AME-PME 0.20. Leg measurements: I: 13.0 (3.80, 4.64, 2.88, 1.68); II: 12.1 (3.44, 4.16, 2.88, 1.60); III: 11.0 (3.20, 3.60, 2.80, 1.36); IV: 14.2 (3.84, 4.72, 3.88, 1.80). Chelicerae with three promarginal, and two retromarginal teeth. Epigynal teeth absent; atrium small; epigynal hoods distinct, situated anteriorly; copulatory ducts short, situated mesad of spermathecae; spermathecal heads small, situated mesad of spermathecae; spermathecae small, slightly extending anteriorly, widely separated (Figs. 28A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Tibet) (Map 9).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius dubius* Wang, sp. nov.**

Figures 29A–D; Map 9

**TYPES.**— Male holotype and female paratype from Pianma Yakou, pass over Gaoligongshan, at elev. 3200m, 25°58'N, 98°41'E, Nujiang Prefecture, Yunnan, China (October 11, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI; 7 female paratypes from Pianma Yakou, Nujiang, Yunnan, China (October 11, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (3 females) and CAS (4 females); 4 male paratypes from native forest in Gaoligongshan at 9.5 road km ESE Pianma, 25°59'N, 98°40'E, el. 2500m, Nujiang Prefecture, Yunnan, China, (October 15–18, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (2 males) and CAS (2 males).

**ETYMOLOGY.**— The specific name refers to the unusual morphology compare to other *Draconarius*: the not spoon-like median apophysis and the absence of epigynal teeth.

**DIAGNOSIS.**— The female of this species is similar to *D. patellabifidus* and *D. simplicidens* by lacking epigynal teeth and having broad spermathecae but can be recognized from *D. simplicidens* by the anteriorly situated spermathecal heads, from *D. patellabifidus* by the broader spermathecal bases and the anteriorly diverging spermathecae (Figs. 29A–B). Male can be recognized by the not spoon-like median apophysis, the bifurcated conductor, and the long patellar apophysis (longer than patellar length) (Figs. 29C–D).

**FEMALE.**— Total length 8.00. Carapace 4.00 long, 2.90 wide. Abdomen 4.00 long, 2.70 wide. Eye sizes and interdistances: AME 0.15, ALE 0.21, PME 0.19, PLE 0.20; AME-AME 0.10, AME-ALE 0.05, PME-PME 0.13, PME-PLE 0.18, AME-PME 0.20. Leg measurements: I: 10.3 (2.90, 3.70, 2.30, 1.40); II: 9.60 (2.70, 3.30, 2.20, 1.40); III: 9.00 (2.40, 3.00, 2.30, 1.30); IV: 12.0 (3.20, 3.80, 3.30, 1.70). Chelicerae with three promarginal, and two retromarginal teeth. Epigynal teeth absent; atrium large; copulatory ducts small, situated mesad of spermathecae; spermathecal heads large, situated anteriorly mesad of spermathecae; spermathecal bases broader than stalks; spermathecal stalks anteriorly diverging (Figs. 29A–B).

**MALE.**— Total length 6.80. Carapace 3.60 long, 2.66 wide. Abdomen 3.20 long, 3.00 wide. Eye sizes and interdistances: AME 0.11, ALE 0.20, PME 0.18, PLE 0.19; AME-AME 0.05, AME-ALE 0.05, PME-PME 0.08, PME-PLE 0.14, AME-PME 0.13. Leg measurements: I: 11.3 (3.10, 3.94, 2.60, 1.70); II: 10.2 (2.80, 3.40, 2.46, 1.52); III: 9.40 (2.70, 2.80, 2.50, 1.40); IV: 12.1 (3.20, 3.80, 3.50, 1.60). Chelicerae with three promarginal, and two retromarginal teeth. Male palp with patellar apophysis longer than patellar length; RTA long; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor broad, bifurcated, with small basal lamella; conductor dorsal apophysis present; embolus prolateral in origin; median apophysis simple, not spoon-like (Figs. 29C–D).

**DISTRIBUTION.**— China (Yunnan) (Map 9).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius episomos* Wang, sp. nov.**

Figures 30A–B; Map 10

**TYPES.**— Female holotype and female paratype from Pianma Yakou, pass over Gaoligong-



shan, at elev. 3200m, 25°58'N, 98°41'E, Nujiang Prefecture, Yunnan, China (October 11, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (female holotype) and CAS (female paratype).

**ETYMOLOGY.**— The specific name refers to the large spermathecae.

**DIAGNOSIS.**— The female is similar to *D. himalayaensis*, *D. altissimus* and *D. subtitanus* in having the short epigynal teeth and rounded, closely situated spermathecae but can be distinguished by the widely separated epigynal teeth (at least one and half atrial width) and the medially situated spermathecal heads. (Figs. 30A–B).

**FEMALE.**— Total length 10.7. Carapace 4.68 long, 2.99 wide. Abdomen 5.98 long, 3.64 wide. Eye sizes and interdistances: AME 0.11, ALE 0.16, PME 0.14, PLE 0.16; AME-AME 0.11, AME-ALE 0.13, PME-PME 0.20, PME-PLE 0.22, AME-PME 0.13. Leg measurements: I: 11.0 (3.23, 3.80, 2.42, 1.51); II: 9.93 (2.86, 3.38, 2.21, 1.48); III: 9.41 (2.55, 3.09, 2.34, 1.43); IV: 12.5 (3.28, 4.16, 3.38, 1.66). Chelicerae with three promarginal, and two retromarginal teeth. Epigynal teeth short, widely separated; atrium small, near epigastric furrow; copulatory ducts small, situated mesad of spermathecae; spermathecal heads small, situated anteriorly mesad of spermathecae; spermathecal bases small, widely separated; spermathecal stalks broad, anteriorly expanded and converging (Figs. 30A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 10).

**OTHER MATERIAL EXAMINED.**— None.

### *Draconarius everesti* (Hu, 2001), NEW COMBINATION

Map 9

*Coeolotes everesti* Hu, 2001:145, figs.8–55:1–3 (male holotype from Ang-Ren, Tibet, China, in SDU, not examined).

**DIAGNOSIS** – The male of this species is similar to *D. singulatus* in having a short cymbial furrow and prolaterally originating embolus but can be distinguished by the short RTA.

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal, and two retromarginal teeth. Male palp with patellar apophysis present; RTA short, much less than half tibial length; cymbial furrow short; conductor short; embolus prolateral in origin; median apophysis spoon-like, slightly elongated. Female unknown.

**DISTRIBUTION.**— China (Tibet) (Map 9).

**MATERIAL EXAMINED.**— None.

### *Draconarius griswoldi* Wang, sp. nov.

Figures 31A–D; Map 11

**TYPES.**— Female holotype and 2 female paratypes from Pianma Yakou, pass over Gaoligongshan, at elev. 3200m, 25°58'N, 98°41'E, Nujiang Prefecture, Yunnan, China (October 11, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (holotype female) and CAS (paratype females); 2 male paratypes from native forest in Gaoligongshan at 9.5 road km ESE Pianma, 25°59'N, 98°40'E, el. 2500m, Nujiang Prefecture, Yunnan, China (October 15–18; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (1 male) and CAS (1 male).

**ETYMOLOGY.**— The specific name is a patronym in honor of Dr. Charles E. Griswold, the collector of the specimens.

**DIAGNOSIS.**— The female of this new species is similar to *D. curiosus* in having the laterally extending copulatory ducts and lacking epigynal teeth but can be easily distinguished by the anteriorly situated spermathecal heads and the unlooped spermathecae (Figs. 31A–B). The male is similar to *D. agrestis* in having a small patellar apophysis, an elongated cymbial furrow, and a posteriorly originated, long embolus but can be distinguished by the slender embolus, the sharp conductor apex, and the slightly spoon-like median apophysis (Figs. 31C–D).

**FEMALE.**— Total length 5.60. Carapace 2.60 long, 1.80 wide. Abdomen 3.00 long, 2.00 wide. Eye sizes and interdistances: AME 0.08, ALE 0.18, PME 0.15, PLE 0.18; AME-AME 0.03, AME-ALE 0.02, PME-PME 0.04, PME-PLE 0.10, AME-PME 0.10. Leg measurements: I: 5.90 (1.72, 2.14, 1.24, 0.80); II: 5.40 (1.58, 1.90, 1.20, 0.72); III: 5.10 (1.40, 1.70, 1.30, 0.70); IV: 6.86 (1.80, 2.30, 1.86, 0.90). Chelicerae with three promarginal, and two retromarginal teeth. Epigynal teeth absent; atrium large; copulatory ducts originating posteriorly laterad of spermathecae, connected to spermathecae anteriorly; spermathecal heads small, situated anteriorly; spermathecal bases broad, widely separated; spermathecal stalks long, anteriorly converging (Figs. 31A–B).

**MALE.**— Total length 5.36. Carapace 2.76 long, 1.80 wide. Abdomen 2.60 long, 1.60 wide. Eye sizes and interdistances: AME 0.07, ALE 0.17, PME 0.15, PLE 0.15; AME-AME 0.04, AME-ALE 0.03, PME-PME 0.05, PME-PLE 0.10, AME-PME 0.07. Leg measurements: I: 7.26 (2.16, 2.50, 1.60, 1.00); II: 6.60 (1.92, 2.20, 1.50, 0.98); III: 5.54 (1.64, 1.60, 1.50, 0.80); IV: 8.10 (2.20, 2.60, 2.20, 1.10). Chelicerae with three promarginal, and two retromarginal teeth. Male palp with patellar apophysis small; RTA long; lateral tibial apophysis present; cymbial furrow more than half cymbial length; conductor broad, with slender apex and large basal lamella; conductor dorsal apophysis broad; embolus posterior in origin; median apophysis broad, elongated, slightly spoon-like (Figs. 31C–D).

**DISTRIBUTION.**— China (Yunnan) (Map 11).

**OTHER MATERIAL EXAMINED.**— None.

### *Draconarius funiushanensis* (Hu, Wang and Wang, 1991), NEW COMBINATION

Map 9

*Coelotes funiushanensis* Hu, Wang and Wang, 1991:41, figs. 14–17 (female holotype, male and female paratypes from Yaochanggou, Neixiang, Henan, China, in SDU, not examined).— Song, Zhu and Chen, 1999:375, figs. 217Q–R, 222B, 223G.

**DIAGNOSIS.**— The female is similar to *D. hui* but can be distinguished by the closely situated spermathecal bases. The male can be easily recognized by the long, lobed patellar apophysis.

**DESCRIPTION.**— See Hu, Wang and Wang (1991). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth near atrium; atrium small; spermathecal bases small, close together; spermathecal stalks broad, anteriorly expanded, close together. Male palpal patellar apophysis large, strongly lobed; RTA long; embolus posterior in origin.

**DISTRIBUTION.**— China (Henan) (Map 9).

**MATERIAL EXAMINED.**— None.

### *Draconarius gurkha* (Brignoli, 1976)

Figures 32A–B; Map 10

*Coelotes gurkha* Brignoli, 1976:239, figs. 13–14 (female holotype from Yak-Alm, Taboche, Nepal, in IZI, Np61–77, examined).

*Draconarius gurkha*: Wang, 2002:67.

**DIAGNOSIS.**— The female is similar to *D. singulatus* by the indistinct spermathecal heads but can be distinguished by the small atrium and the indistinct copulatory ducts (Figs. 32A–B).

**DESCRIPTION.**— See Brignoli (1976). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth situated near atrium; atrium small, near epigastric furrow; copulatory ducts invisible from dorsal view; spermathecal bases narrow, widely separated; spermathecal stalks broad, rounded (Figs. 32A–B). Male unknown.

**DISTRIBUTION.**— Nepal (Fig. Map 10).

**MATERIAL EXAMINED.**— NEPAL: Taboche (= Taweche), Yak-Alm, Zwergstranchheideboden, 4550 m, May 31, 1961, female holotype (H. Janetschek, IZI, Np61–77); Mingbo-Tal beim Airstrip der Hillary-Makalu Expedition, 4800 m, May 28, 1961, female type of *Coelotes lama* Brignoli, 1976 (IZI, Np61–71).

***Draconarius gyринiformis* (Wang and Zhu, 1991), NEW COMBINATION**

Map 10

*Coelotes gyринiformis* Wang and Zhu, 1991:4, figs. 11–12 (female holotype, 1 female paratype from Kangding, Sichuan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:375, figs. 217Y–Z.

**DIAGNOSIS.**— The female of this species is similar to *D. wudangensis* in having medially situated and widely separated epigynal teeth, and similar spermathecal tubes but can be distinguished by laterally situated spermathecal heads.

**DESCRIPTION.**— See Wang and Zhu (1991). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth widely separated, anterior of atrium; atrium small, near epigastric furrow; spermathecal bases small, widely separated; spermathecal stalks broad, anteriorly expanded and converging. Male unknown.

**DISTRIBUTION.**— China (Sichuan) (Map 10).

**MATERIAL EXAMINED.**— None.

***Draconarius haopingensis* Wang, sp. nov.**

Figures 33A–B; 96A; Map 10

**TYPES.**— Female holotype and female paratype from Haoping, Taibaishan, Shaanxi, China (August 11, 1989; X.P. Wang), deposited in IZB.

**ETYMOLOGY.**— The specific name refers to the type locality.

**DIAGNOSIS.**— The female of this new species is similar to *D. molluscus* by lacking epigynal teeth and having laterally situated epigynal hoods but can be distinguished by the single loop of copulatory ducts and the smooth, non-convoluted spermathecal distal ends (Figs. 33A–B).

**FEMALE.**— Total length 5.19. Carapace 2.28 long, 1.76 wide. Abdomen 2.91 long, 1.89 wide. Eye sizes and interdistances: AME 0.12, ALE 0.14, PME 0.14, PLE 0.15; AME–AME 0.08, AME–ALE 0.05, PME–PME 0.11, PME–PLE 0.13. Leg measurements: I: 7.18 (1.94, 2.61, 1.69, 0.94); II: 6.43 (1.81, 2.31, 1.40, 0.79); III: 5.68 (1.64, 1.85, 1.40, 0.79); IV: 7.76 (2.20, 2.59, 2.06, 0.91). Chelicerae with three promarginal and three retromarginal teeth. Epigynal teeth absent; atrium large; epigynal hoods situated posteriorly, laterad of atrium; copulatory ducts broad, originating posteriorly, extending mesad of spermathecae, looped around spermathecae; spermathecal bases widely separated; spermathecal stalks long, anteriorly converging (Figs. 33A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Shaanxi) (Map 10).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius hangzhouensis* (Chen, 1984), NEW COMBINATION**

Figures 34A–B; Map 11

*Coelotes hangzhouensis* Chen, 1984:1, figs. 1–2 (female holotype from Yunqi, 1 female paratype from Huanglongdong, Hangzhou, Zhejiang, China, in HTC, examined).—Chen and Zhang, 1991:188, figs. 186.1–2;—Song, Zhu and Chen, 1999:375, figs. 217A–B.

**DIAGNOSIS.**— This species can be easily recognized by the trifurcated, less sclerotized anterior atrial margin, the broad, anteriorly extending copulatory ducts, and the long, large spermathecal heads of the female (Fig. 34A–B).

**DESCRIPTION.**— See Chen (1984). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated anteriorly; anterior atrial margin modified into three broad, less sclerotized pieces; atrium small, near epigastric furrow; copulatory ducts broad, originating posteriorly, mesad of spermathecae, extending anteriorly anterad of spermathecae; spermathecal heads large, anteriorly extending; spermathecae broad, widely separated (Figs. 34A–B). Male unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 11).

**MATERIAL EXAMINED.**— CHINA: Zhejiang: Hangzhou, Yunqi, October 7, 1981, female holotype (Z.F. Chen, HTC); Huanglongdong, October 7, 1979, 1 female paratype (Z.F. Chen, HTC).

***Draconarius himalayaensis* (Hu, 2001), NEW COMBINATION**

Map 11

*Coelotes himalayaensis* Hu, 2001:134, figs. 8–45:1–4 (female holotype, male and female paratypes from Linzhi, Tibet, China, in SDU, not examined).

**DIAGNOSIS.**— The female is similar to *D. altissimus* and *D. subtitanus* in having the short epigynal teeth, anteriorly situated spermathecal heads and rounded, closely situated spermathecae but can be distinguished by the epigynal teeth position (widely separated with atrium). The male is similar to *D. patellabifidus* in having a bifurcate patellar apophysis and simple median apophysis but can be distinguished by the slightly notched embolic base and the less apparent cymbial furrow (the cymbial furrow might have been ignored in the original illustration).

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth small, widely separated; atrium small; copulatory ducts long, slender, anteriorly extending; spermathecal heads situated anteriorly; spermathecae broad, rounded, close together. Male palpal patellar apophysis strongly bifurcate, with ventral one large and dorsal one small; RTA almost tibial length; lateral tibial apophysis present; cymbial furrow short; conductor short, anteriorly extending, with small basal lamella; conductor dorsal apophysis short; embolus broad, prolateral in origin; embolic base slightly notched; median apophysis long, broad, not spoon-like.

**DISTRIBUTION.**— China (Tibet) (Map 11).

**MATERIAL EXAMINED:** CHINA: **Tibet:** Jala (SE Tibet), 29.42°N, 94.54°E, 2900 m., April 29, 1998, 3 females (G. Schaller, AMNH).

***Draconarius hui* (Dankittipakul and Wang, 2003), NEW COMBINATION**

Map 12

*Coelotes wangi* Hu, 2001:133, figs. 8–44:1–2 (female holotype, 2 female paratypes from Sejilashan, Linzhi, Tibet, China, in SDU, not examined). This specific name is preoccupied by Chen and Zhao, 1997. *Coelotes hui* Dankittipakul and Wang, 2003:13. (replacement name).

**DIAGNOSIS.**— The female of this species is similar to *D. funiushanensis* but can be distinguished by the widely separated spermathecal bases.

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal, and two retromarginal teeth. Female with epigynal teeth situated near atrium; atrium large; copulatory ducts originating posteriorly, extending mesad of spermathecae; spermathecal bases small, widely separated; spermathecal bases broad, anteriorly expanded and converging. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 12).

**MATERIAL EXAMINED.**— None.

***Draconarius huizhunesis* (Wang and Xu, 1988), NEW COMBINATION**

Map 11

*Coelotes huizhunesis* Wang and Xu, 1988:7, figs. 1–5 (female holotype, male and female paratypes from Qiyun Mt., Aihui, China, in HTC, not examined).— Platnick, 2000–2002.

*Coelotes huizhunesis*: Wang and Xu, 1988: 4 (invalid name, Platnick, 2000–2002).

*Coelotes huizhouensis* Song, Zhu and Chen, 1999:375, figs. 219O–P, 222E, 223H (invalid emendation, Platnick, 2000–2002)

**DIAGNOSIS.**— The female of this species is similar to *D. strophadatus* in having long epigynal teeth but can be distinguished by the widely separated and anteriorly converging spermathecal stalks. The male is similar to *D. ornatus* in having a bifurcate conductor but can be recognized by the slender embolus and the strongly elongated cymbial furrow.

**DESCRIPTION.**— See Wang and Xu (1988). Chelicerae with three promarginal, and two retromarginal teeth. Female with epigynal teeth situated anteriorly, close together, strongly elongated; spermathecal bases small, close together; spermathecal stalks extending laterally, widely separated, convoluted, and anteriorly converging. Male palpal patellar apophysis present; RTA long; lateral tibial apophysis widely separated from RTA; cymbial furrow short; conductor bifurcate; conductor dorsal apophysis present; median apophysis spoon-like, rounded; embolic base narrow; embolus long, posterior in origin.

**DISTRIBUTION.**— China (Aihui) (Map 11).

**MATERIAL EXAMINED.**— None.

***Draconarius incertus* Wang, sp. nov.**

Figures 35A–B; Map 12

**TYPES.**— Male holotype and 4 male paratypes from native forest in Gaoligongshan at 9.5 road km ESE Pianma, 25°59'N, 98°40'E, el. 2500 m, Nujiang Prefecture, Yunnan, China (October 15–18, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (holotype male and 2 paratype males) and CAS (2 paratype males).

**ETYMOLOGY.**— The specific name refers to the uncertain generic placement because of the not spoon-like median apophysis and the prolaterally originated embolus.

**DIAGNOSIS.**— The male of this new species is similar to *D. dubius* but can be recognized by the short patellar apophysis (Figs. 35A–B).

**MALE.**— Total length 8.00. Carapace 4.00 long, 2.80 wide. Abdomen 4.00 long, 2.60 wide. Eye sizes and interdistances: AME 0.14, ALE 0.20, PME 0.17, PLE 0.19; AME-AME 0.06, AME-ALE 0.05, PME-PME 0.12, PME-PLA 0.15, AME-PME 0.12. Leg measurements: I: 17.7 (4.40, 5.70, 4.50, 3.10); II: 16.0 (4.00, 5.00, 4.10, 2.90); III: 14.2 (3.70, 4.30, 4.00, 2.20); IV: 19.1 (4.60,

5.56, 6.00, 2.90). Chelicerae with three promarginal and two retromarginal teeth. Male palp with short patellar apophysis; RTA long; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor slender, with apex slightly bifurcate; conductor dorsal apophysis slender; conductor lamella small; embolus prolateral in origin; median apophysis large, not spoon-like (Figs. 35A–B).

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 12).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius infulatus* (Wang et al., 1990)**

Map 12

*Coelotes infulatus* Wang et al., 1990:202, figs. 57–58 (female holotype and female paratype from Tianmushan, Zhejiang, China, in HBI, not examined).— Song, Zhu and Chen, 1999:375, figs. 220F–G.

*Draconarius infulatus*: Wang 2002:67.

**DIAGNOSIS.**— The female of this species can be easily distinguished from other coelotines by the posteriorly situated, widely separated epigynal teeth and the broad, anteriorly expanded, overlapped copulatory ducts.

**DESCRIPTION.**— See Wang et al. (1990). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth widely separated, situated posteriorly near atrium; atrium broad, near epigynal furrow; copulatory ducts broad, posteriorly originating, anteriorly expanded, connected to spermathecae laterally; spermathecae small, enclosed by copulatory ducts. Male unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 12).

**MATERIAL EXAMINED.**— None.

***Draconarius jiangyongensis* (Peng, Gong and Kim, 1996), NEW COMBINATION**

Figures 36A–B; 96B; Map 12

*Coelotes jiangyongensis* Peng, Gong and Kim, 1996:19, figs. 7–9 (female holotype, 4 female paratypes from Qianjiaotong, Jiangyong, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:376, figs. 220J–K.

**DIAGNOSIS.**— This species can be easily recognized by the vase-shaped epigynal plate, the long, anteriorly extending copulatory ducts, and the long, wedge-shaped spermathecae of female (Fig. 36A–B).

**DESCRIPTION.**— See Peng, Gong and Kim (1996). Cheliceral promargin with three teeth, retromargin four. Female epigynal teeth short, widely separated; atria separated by the median septum that spaced wider apart posteriorly than anteriorly; copulatory ducts long, anteriorly extending along with spermathecae; spermathecal heads small, anteriorly situated and laterally extending; spermathecal bases broad, widely separated; spermathecal stalks long, wider apart posteriorly and converged together anteriorly (Figs. 36A–B). Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 12).

**MATERIAL EXAMINED.**— CHINA: **Hunan**: Jiangyong, Qianjiaotong, October 1, 1991, female holotype and 4 female paratypes (N.S. Gong, HBI).

***Draconarius labiatus* (Wang and Ono, 1998)**

Figures. 37A–B; Map 13

*Coelotes labiatus* Wang and Ono, 1998:145, figs. 8–9 (female holotype and 1 female paratype from Nantou Hsien, Taiwan, China, in NSMT, examined).

*Draconarius labiatus*: Wang, 2002:67.

**DIAGNOSIS.**— This species is similar to *D. wenzhouensis* but can be distinguished by the small, dorsally covered spermathecal heads and the transversely extending spermathecal expansions (Fig. 37A–B).

**DESCRIPTION.**— See Wang and Ono (1998). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth short, anteriorly situated, adjacent; atrium situated posteriorly near epigastric furrow, with anterior atrial margin expanded, lip-shaped; copulatory ducts slightly sclerotized, originating posteriad, extending mesad of spermathecae; spermathecal heads small, covered by copulatory ducts in dorsal view; spermathecal bases widely separated; spermathecal stalks extending anteriorly, then curved and extending (Figs. 37A–B). Male unknown.

**DISTRIBUTION.**— China (Taiwan) (Map 13).

**MATERIAL EXAMINED.**— CHINA: **Taiwan:** Nantou Hsien, Tatachia, 2100 m alt., March 5, 1991, female holotype (H. Ono, NSMT, NSMT-Ar.3436); Nantou Hsien, Shemu, Mt. Hohuan-shan, 2180 m alt., March 12, 1991, 1 female paratype (H. Ono, NSMT, NSMT-Ar.3444).

### *Draconarius linzhiensis* (Hu, 2001), NEW COMBINATION

Map 13

*Coelotes linzhiensis* Hu, 2001:138, figs. 8–48:1–2 (female holotype and paratypes from Linzhi, Tibet, China, in SDU, not examined).

**DIAGNOSIS.**— The female is similar to *D. qingzangensis* in having the similar spermathecal tubes but can be distinguished by the slightly separated atria and the moderately expanded anterior spermathecae (same width as stalks).

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth situated laterad of atrium; atrium large; spermathecal heads situated medially on spermathecae; spermathecal bases widely separated; spermathecal stalks broad, anteriorly expanded and converging. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 13).

**MATERIAL EXAMINED.**— None.

### *Draconarius linxiaensis* Wang, sp. nov.

Figures 38A–B; Map 13

**TYPES.**— Male holotype from Linxia, Gansu, China (August 30, 1997; X.P. Wang), deposited in IZB.

**ETYMOLOGY.**— The specific name refers to the type locality.

**DIAGNOSIS.**— The male of this new species is similar to *D. neixiangensis* in lacking a patellar apophysis and having a broad, deeply grooved conductor but can be distinguished by the broad median apophysis and the slender embolic base and apex (Figs. 38A–B).

**MALE.**— Total length 7.80. Carapace 4.00 long, 2.72 wide. Abdomen 3.80 long, 2.00 wide. Eye sizes and interdistances: AME 0.14, ALE 0.17, PME 0.15, PLE 0.17; AME-AME 0.06, AME-ALE 0.05, PME-PME 0.13, PME-PLE 0.17, AME-PME 0.12. Leg measurements: I: 12.3 (3.20, 4.20, 2.92, 2.00); II: 11.3 (3.00, 3.80, 2.88, 1.60); III: 10.7 (2.80, 3.36, 3.00, 1.52); IV: 14.3 (3.20, 4.40, 4.32, 2.40). Cheliceral promargin with three teeth, retromargin with two. Male palp lacking

patellar apophysis; RTA long; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor broad, deeply grooved; conductor dorsal apophysis broad; embolus long, broad, posterior in origin, with narrow base and slender, bifurcate apex; median apophysis broad, spoon-like (Figs. 38A–B).

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Gansu) (Map 13).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius lutulentus* (Wang et al., 1990)**

Figures 39A–E; 40A–H; Map 13

*Coelotes lutulentus* Wang et al., 1990:216, figs. 88–92 (2 male and 2 female paratypes, holotype not indicated, from Zhangjiajie, Dayong, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:376, figs. 220R–S, 222K, 223N; —Hu, 2001:139, figs. 8–49:1–4.

*Coelotes sinualis* Chen, Zhao and Wang, 1991:10, figs. 3, 4 (female holotype from Jinding, Wudangshan, Hubei, China, in HUW, examined);— Song, Zhu and Chen, 1999:378, figs. 224T, U. **NEW SYNONYMY.**

*Draconarius sinualis*: Wang, 2002:72, figs. 192–210.

*Draconarius lutulentus*: Wang, 2002:12.

**DIAGNOSIS.**— The female of this species is similar to *D. wuermlii* but can be distinguished by the strongly convoluted spermathecae and the differences in shapes between their atria (Figs. 39A–B; 40A–B, E–F). The male is similar to *D. wudangensis* in having the short RTA but can be recognized by the long, slender conductor (Figs. 39C–E; 40C–D, G–H).

**SYNONYMY.**— This species is widespread in central and eastern China, with variable male and female genitalic morphology. The species *D. sinualis*, described from Wudangshan, Hubei, China, has the identical genitalic morphology and is placed as a junior synonym of *D. lutulentus*.

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retro-marginal three. Epigynal teeth short, situated laterally, near atrium; atrium small; copulatory ducts long, originating posteriorly, extending mesad of spermathecae, looped around distal spermathecae; spermathecal heads small; spermathecal bases widely separated; spermathecal stalks long, anteriorly converging (Figs. 39A–B; 40A–B, E–F). Male palp with large patellar apophysis; RTA short, approximately half tibial length; lateral tibial apophysis large; cymbial furrow long, about half tibial length or longer; conductor long, slender, with large basal lamella; conductor dorsal apophysis slender; embolus posterior in origin; median apophysis spoon-like, elongated (Figs. 39C–E; 40C–D, G–H).

**DISTRIBUTION.**— China (Hubei, Hunan, Shaanxi, Tibet, Zhejiang, Anhui) (Map 13).

**MATERIAL EXAMINED.**— **CHINA:** **Hubei:** Wudangshan, Jinding, April 23, 1982, female holotype of *Coelotes sinualis* Chen, Zhao and Wang, 1991 (HUW); Wudangshan, Jinding, September 24, 1997, 3 females, 1 male and 2 females (X.P. Wang, AMNH); Wudangshan, Nanya to Jinding, September 24, 1997, 1 male and 1 female, 1 female, 11 females and 3 males (X.P. Wang, IZB); Wudangshan, Zhixiao to Nanya, September 23, 1997, 3 females and 7 males (X.P. Wang, MCB); Hongping, September 21, 1997, 2 males and 9 females (X.P. Wang, IZB). **Hunan:** Dayong, Zhangjiajie, October 17, 1984, 2 male and 2 female paratypes (J.F. Wang and Y.J. Zhang, HBI). **Shaanxi:** Huxian, Cuihuashan, October 18, 1989, 1 male and 1 female (X.P. Wang, IZB).

***Draconarius magniceps* (Schenkel, 1936), NEW COMBINATION**

Figure 41A–B; Map 14



*Coelotes magniceps* Schenkel, 1936:186, fig. 61 (female holotype from Kina, S. Gansu, China, in NRS, examined).— Song, Zhu and Chen, 1999:376.

**DIAGNOSIS.**— The female of this species can be easily recognized by the absence of epigynal teeth, the presence of a broad atrial septum, and the large, anteriorly expanded copulatory ducts (Figs. 41A–B).

**DESCRIPTION.**— Described by Schenkel (1936). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth absent; atrium large, with broad septum; copulatory ducts broad, extending anteriorly; spermathecal heads small, anteriorly situated; spermathecae broad, short, slightly separated (Figs. 41A–B). Male unknown.

**DISTRIBUTION.**— China (Gansu) (Map 14).

**MATERIAL EXAMINED.**— CHINA: **Gansu:** Kina, female holotype (Dr. Hummel, NRS, burk 6, Sven Hedins Exp. Ctr. Asien).

### *Draconarius molluscus* (Wang et al., 1990)

Figure 42A–B; 96D; Map 14

*Coelotes molluscus* Wang et al., 1990:214, figs. 86–87 (4 female types, holotype not indicated, from Lushan, Jiangxi, China, in HBI, examined).— Song, Zhu and Chen, 1999:376, figs. 221G–H.

*Draconarius molluscus*: Wang, 2002:67.

**DIAGNOSIS.**— The female of this species is similar to *D. haopingensis* in lacking the epigynal teeth and having the laterally situated epigynal hoods but can be distinguished by the presence of two copulatory duct loops and the convoluted spermathecal distal ends (Fig. 42A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retromargin three. Female without epigynal teeth; atrium broad; epigynal hoods deep, situated posteriorly, laterad of atrium; copulatory ducts long, originating posteriorly, mesad of spermathecae, looped around spermathecae; spermathecal heads small; spermathecal bases widely separated; spermathecal stalks long, anteriorly converging (Figs. 42A–B). Male unknown.

**DISTRIBUTION.**— China (Jiangxi) (Map 14).

**MATERIAL EXAMINED.**—CHINA: **Jiangxi:** Lushan, June 15, 1987, 4 female types (J.F. Wang, HBI).

### *Draconarius nanyuensis* (Peng and Yin, 1998), NEW COMBINATION

Figures 43A–B; Map 14

*Coelotes nanyuensis* Peng and Yin, 1998:27, figs. 7–9 (female holotype from Nanyue, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:376.

**DIAGNOSIS.**— The female of this species can be easily distinguished by the adjacent, anteriorly situated epigynal teeth, the separated atria, and the rounded spermathecae (Figs. 43A–B).

**DESCRIPTION.**— Described by Peng and Yin (1998). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth short, situated anteriorly, adjacent; atria small, distinctly separated; copulatory ducts narrow, originating posteriorly, extending mesad of spermathecae; spermathecal heads anteriorly situated; spermathecae large, rounded, slightly separated (Figs. 43A–B). Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 14).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Nanyue, August 3–7, 1995, female holotype (C.M. Yin, HBI).

***Draconarius neixiangensis* (Hu, Wang and Wang, 1991)**

Figures 44A–D; Map 14

*Coelotes neixiangensis* Hu, Wang and Wang, 1991:43, figs. 18–21 (female holotype, male and female paratypes from Neixiang, Henan, China, deposited in SDU, not examined).— Song, Zhu and Chen, 1999:377, figs. 221K–L, 222N, 224B.

*Coelotes baccatus* Wang, 1994:286, figs. 1–5 (2 male and 2 female types from Xiangfan, Hubei, China, in HBI, examined).— Song, Zhu and Chen, 1999:374, figs. 216P–Q, 218E, L. NEW SYNONYMY.

*Draconarius baccatus*: Wang, 2002:66.

*Draconarius neixiangensis*: Wang, 2002:68.

**DIAGNOSIS.**— The female of this species can be easily recognized by the anteriorly situated epigynal teeth, the broad, posteriorly situated atrium, and the broad, anteriorly expanded copulatory ducts (Figs. 44A–B). The male is similar to *D. linxiaensis* in lacking a patellar apophysis and having the broad, deeply grooved conductor but can be distinguished by the elongated, slender median apophysis and the broad embolic base and apex (Figs. 44C–D).

**DESCRIPTION.**— Described by Chen (1984) and Wang (1994). Chelicerae with three promarginal and two retromarginal teeth. Female epigynal teeth short, situated anteriorly, close together; atrium broad, near epigastric furrow, with anterior margin slightly notched into two broad, less sclerotized pieces; copulatory ducts broad, originating posteriorly, strongly expanded anteriorly; spermathecal heads small, situated laterally on ventral side of spermathecae; spermathecal bases small, widely separated; spermathecal stalks short, anteriorly diverging (Figs. 44A–B). Male palp without patellar apophysis; RTA long; lateral tibial apophysis widely separated from RTA; cymbial furrow short; conductor broad, strongly grooved, with small basal lamella; conductor dorsal apophysis small; embolus broad, posterior in origin, with slightly modified apex; median apophysis spoon-like, elongated (Figs. 44C–D).

**DISTRIBUTION.**— China (Henan, Hubei) (Map 14).

**MATERIAL EXAMINED.**— CHINA: **Hubei**: Xiangfan, October 26, 1990, 2 male and 2 female types of *Coelotes baccatus* (J.F. Wang, HBI).

***Draconarius nudulus* Wang, sp. nov.**

Figures 45A–B; Map 15

**TYPES.**— Male holotype from 36 air km SE TengChong, pass over Gaoligongshan at 2100 m, 24°50'N, 98°47'E, Nankang, Baoshan, Yunnan, China (November 4–7, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI.

**ETYMOLOGY.**— The specific name refers to the absence of patellar apophysis.

**DIAGNOSIS.**— The male of this new species is similar to *D. argenteus* in lacking a patellar apophysis and having a short conductor but can be distinguished by the long RTA (more than half tibial length), the simple median apophysis, and the non-lobed embolic base (Figs. 45A–B).

**MALE.**— Total length 6.14. Carapace 3.14 long, 1.94 wide. Abdomen 3.00 long, 2.30 wide. Eye sizes and interdistances: AME 0.08, ALE 0.16, PME 0.15, PLE 0.15; AME-AME 0.04, AME-ALE 0.04, PME-PME 0.15, PME-PLE 0.15, AME-PME 0.10. Leg measurements: I: 8.68 (2.40, 3.08, 1.96, 1.24); II: 7.36 (2.08, 2.40, 1.76, 1.12); III: 6.70 (1.86, 2.06, 1.80, 0.98); IV: 9.30 (2.46, 3.00, 2.64, 1.20). Promargin of chelicera with three teeth, retromargin one. Male palp without patellar apophysis; RTA approximately tibial length or slightly longer; lateral tibial apophysis near RTA; cymbial furrow short; conductor short; conductor dorsal apophysis broad; conductor lamella small; embolus posterior in origin; median apophysis strongly elongated, slightly or not spoon-like (Figs. 45A–B). Female unknown.

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 15).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius ornatus* (Wang et al., 1990), NEW COMBINATION**

Figures 46A–C; 96C; Map 15

*Coelotes ornatus* Wang et al., 1990:199, figs. 53–54 (female holotype and paratypes from Xishan, Kunming, Yunnan, China, in HBI, not examined).— Song, Zhu and Chen, 1999:377, figs. 221O–P.

**DIAGNOSIS.**— The female of this species is similar to *D. terebratus* by lacking epigynal teeth, having posteriorly situated epigynal hoods, anteriorly extending copulatory ducts, and long spermathecal heads but can be distinguished by the slightly elongated atrium and the less broad spermathecal bases. The male is similar to *D. huizhunesis* by having a bifurcate conductor but can be distinguished by the broad embolus and the short cymbial furrow (Fig. 46A–C).

**NOTES.**— Although the female types could not be located, two males labeled as *C. ornatus* were found in HBI collection. Further collection of this species is badly needed in order to verify this association.

**DESCRIPTION.**— The female was described by Wang et al. (1990), and the male is described for the first time. Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth absent; atrium large; epigynal hoods situated posteriorly, laterad of atrium; copulatory ducts posteriorly originating, strongly expanded anteriorly; spermathecal heads long, slender, anteriorly extending; spermathecal bases small, widely separated; spermathecal stalks anteriorly diverging. Male palp with patellar apophysis long; RTA small; lateral tibial apophysis widely separated from RTA; cymbial furrow short; conductor long, broad, with bifurcate apex and small basal lamella; conductor dorsal apophysis small; embolus broad, posterior in origin; median apophysis small, spoon-like (Figs. 46A–C).

**DISTRIBUTION.**— China (Yunnan) (Map 15).

**MATERIAL EXAMINED.**— CHINA: **Yunnan:** Kunming, Xishan, August 8, 1991, 2 males (HBI).

***Draconarius parabrunneus* Wang, sp. nov.**

Figures 47A–B; 96E; Map 15

**TYPES.**— Female holotype, 4 female paratypes from native forest in Gaoligongshan at 9.5 road km ESE Pianma, 25°59'N, 98°40'E, el. 2500 m, Gaoligongshan, Nujiang Prefecture, Yunnan, China (October 15–18, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (holotype and 2 paratype females) and CAS (2 paratype females).

**ETYMOLOGY.**— The specific name refers to its similarity to *D. brunneus* related species.

**DIAGNOSIS.**— The female of this species is similar to *D. pseudobrunneus* in lacking the epigynal teeth and having small, broad spermathecae but can be distinguished by the anteriorly situated spermathecal heads and the broad spermathecal bases (broader than stalks) (Figs. 47A–B).

**FEMALE.**— Total length 10.3. Carapace 4.30 long, 2.80 wide. Abdomen 6.00 long, 4.00 wide. Eye sizes and interdistances: AME 0.13, ALE 0.22, PME 0.20, PLE 0.20; AME-AME' 0.10, AME-ALE 0.04, PME-PME 0.13, PME-PL 0.13, AME-PME 0.14. Leg measurements: I: 12.8 (3.60, 4.30, 2.90, 2.00); II: 11.6 (3.30, 3.80, 2.76, 1.70); III: 10.6 (3.00, 3.20, 2.80, 1.60); IV: 14.3 (3.60, 4.56, 4.10, 2.00). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth absent; atrium small; epigynum wrinkly on anterior atrium; copulatory ducts short, situated

mesad of spermathecae; spermathecal heads situated anteriorly; spermathecal bases broad, widely separated; spermathecal stalks short (Figs. 47A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 15).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius paraterebratus* Wang, sp. nov.**

Figures 48A–B; Map 16

**TYPES.**— Female holotype from pass over Gaoligongshan at 2300 m, Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, TengChong, Luoshuidong, Baoshan, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI.

**ETYMOLOGY.**— The specific name refers to its similarity to *D. terebratus*.

**DIAGNOSIS.**— The female of this species can be easily recognized by the posteriorly situated epigynal teeth and the presence of diverticula on spermathecal bases (Figs. 48A–B).

**FEMALE.**— Total length 11.2. Carapace 5.00 long, 3.20 wide. Abdomen 6.20 long, 4.20 wide. Eye sizes and interdistances: AME 0.25, ALE 0.24, PME 0.24, PLE 0.24; AME-AME 0.10, AME-ALE 0.10, PME-PME 0.20, PME-PL 0.26, AME-PME 0.25. Leg measurements: I: 13.5 (3.82, 4.64, 3.28, 1.80); II: 11.9 (3.50, 4.02, 2.82, 1.58); III: 10.3 (3.04, 3.22, 2.76, 1.30); IV: 13.5 (3.82, 4.32, 3.70, 1.70). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth small, situated posteriorly laterad of atrium; atrium broad; copulatory ducts broad, long, originating anteriorly, overlapped dorsally with spermathecal stalks; spermathecal heads anteriorly situated; spermathecal bases slightly separated, with long diverticula; spermathecal stalks long, widely separated (Figs. 48A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Fig. Map 16).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius patellabifidus* Wang, sp. nov.**

Figures 49A–D; Map 17

**TYPES.**— Male holotype, 2 male and 4 female paratypes from Dulong/Gongshan Yakou area, Nujiang State Nature Reserve, Nujiang Prefecture, Gaoligong Shan, Yunnan, China (July 16–17, 2000; H.M. Yan, D. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong), deposited in HBI (male holotype, 1 male and 3 female paratype) and CAS (1 male and 1 female paratypes); 1 female paratype from Nujiang State Nature Reserve, Dulong/Gongshan Yakou area, 21 airkm W of Gongshan, N27.697°/E98.454°, 3300–3680m, Gaoligong Shan, Nujiang Prefecture, Yunnan, China (July 16–17, 2000; H.M. Yan, D. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D.Z. Dong), deposited in CAS; 9 male paratypes from Pianma, Yakou, Pass over Gaoligongshan at el. 3200 m, 25°58'N, 98°41'E, bamboo thicket and under stones, Nujiang Prefecture, Yunnan, China (October 11, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI (4 males) and CAS (5 males).

**ETYMOLOGY.**— The specific name refers to the bifurcate patellar apophysis.

**DIAGNOSIS.**— The female of this species is similar to *D. dubius* and *D. simplicidens* by lacking epigynal teeth and having broad spermathecae but can be recognized from *D. simplicidens* by the anteriorly situated spermathecal heads, from *D. dubius* by the less expanded spermathecal bases (smaller than stalks) (Figs. 49A–B). The male is similar to *D. himalayaensis* by having the bifur-

cate patellar apophysis and the simple median apophysis but can be distinguished by the entire embolic base and the presence of distinct cymbial furrow (Figs. 49C–D).

**FEMALE.**— Total length 10.4. Carapace 5.20 long, 3.51 wide. Abdomen 5.20 long, 3.38 wide. Eye sizes and interdistances: AME 0.15, ALE 0.25, PME 0.20, PLE 0.20; AME–AME 0.13, AME–ALE 0.10, PME–PME 0.15, PME–PLE 0.25, AME–PME 0.23. Leg measurements: I: 13.2 (3.64, 4.58, 3.07, 1.95); II: 12.2 (3.38, 4.16, 2.81, 1.82); III: 11.5 (3.02, 3.85, 2.94, 1.69); IV: 14.7 (3.77, 4.89, 3.98, 2.05). Promargin of chelicera with three teeth, retromargin with two. Epigynal teeth absent; atrium small; copulatory ducts small, originating posteriorly, extending mesad of spermathecae; spermathecal heads situated anteriorly; spermathecae broad, widely separated (Figs. 49A–B).

**MALE.**— Total length 11.8. Carapace 6.11 long, 4.21 wide. Abdomen 5.72 long, 3.64 wide. Eye sizes and interdistances: AME 0.19, ALE 0.26, PME 0.23, PLE 0.24; AME–AME 0.11, AME–ALE 0.06, PME–PME 0.15, PME–PLE 0.20, AME–PME 0.18. Leg measurements: I: 21.5 (5.51, 7.07, 5.59, 3.28); II: 19.8 (5.20, 6.50, 5.20, 2.91); III: 17.6 (4.55, 5.59, 4.81, 2.60); IV: 21.7 (5.59, 6.76, 6.24, 3.07). Promargin of chelicera with three teeth, retromargin with two. Palpal patellar apophysis strongly bifurcate, with ventral one large and dorsal one small; RTA long; lateral tibial apophysis wide apart from RTA; cymbial furrow short; conductor short, anteriorly extending, with bifid apex and small basal lamella; conductor dorsal apophysis short; embolus broad, prolateral in origin; median apophysis long, not spoon-like (Figs. 49C–D).

**DISTRIBUTION.**— China (Yunnan) (Map 17).

**OTHER MATERIAL EXAMINED.**— None.

### *Draconarius penicillatus* (Wang et al., 1990), NEW COMBINATION

Figures 50A–E; Map 16

*Caelotes penicillatus* Wang et al., 1990:197, figs. 48–52 (female holotype and male paratype from Xishan, Kunming, Yunnan, China, in HBI, examined).

*Caelotes penicilatus* Song, Zhu and Chen, 1999:377, figs. 221U–V, 223A, 224E.

**DIAGNOSIS.**— The female of this species can be easily identified by the anteriorly situated copulatory ducts and the laterally extending spermathecae (Fig. 50A–B). The male is similar to *D. coreanus* but can be recognized by the posteriorly extending conductor and the short embolic base (Figs. 50C–E).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth small, situated near atrium; atrium small; copulatory ducts broad, anteriorly situated, convoluted around spermathecal heads; spermathecal heads anteriorly situated; spermathecal bases small; spermathecal stalks extending laterally (Figs. 50A–B). Male palp with small patellar apophysis; RTA long; lateral tibial apophysis large; cymbial furrow more than half cymbial length; conductor short, posteriorly extending, with small basal lamella; conductor dorsal apophysis broad; embolus long, posterior in origin; embolic base short; median apophysis small, rounded; spoon-like (Figs. 50C–E).

**DISTRIBUTION.**— China (Yunnan) (Map 16).

**MATERIAL EXAMINED.**— CHINA: **Yunnan:** Kunming, Xishan, October 24, 1987, female holotype and male paratype (J. F. Wang, HBI).

### *Draconarius pervicax* (Hu and Li, 1987), NEW COMBINATION

Map 15

*Caelotes pervicax* Hu and Li, 1987:279, figs. 18.5–6 (female holotype from Yadong, Tibet, China, in SDU, not examined).— Song, Zhu and Chen, 1999:377, figs. 221W–X;— Hu, 2001:141, figs. 8–51:1–2.

**DIAGNOSIS.**— The female of this species is similar to *D. quadratus* but can be distinguished by the closely situated spermathecal bases.

**DESCRIPTION.**— See Hu and Li (1987). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth situated laterad of atrium; atrium broad; spermathecal bases large, close together; spermathecal stalks widely separated, anteriorly elongated. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 15).

**MATERIAL EXAMINED.**— None.

***Draconarius picta* (Hu, 2001), NEW COMBINATION**

Map 16

*Coelotes picta* Hu, 2001:142, figs. 8–52:1–2 (female holotype and 2 female paratypes from Sejilashan, Linzhi, Tibet, China, in SDU, not examined).

**DIAGNOSIS.**— The female is similar to *D. wudangensis* in having the medially situated and widely separated epigynal teeth, and similar spermathecal tubes but can be distinguished by the closely situated spermathecae and the slender spermathecal bases.

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth widely separated, situated posteriorly near epigastric furrow; atrium small; spermathecal heads small; spermathecal bases slightly separated; spermathecal stalks broad, anteriorly expanded and converging. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 16).

**MATERIAL EXAMINED.**— None.

***Draconarius potanini* (Schenkel, 1963)**

Figures 51A–B; Map 16

*Cybaeus potanini* Schenkel, 1963:275, fig. 156 (female holotype from Gansu, China, in MNHN, examined).— Song, Zhu and Chen, 1999:355, figs. 208I–J.

*Draconarius potanini*: Wang, 2002:68.

**DIAGNOSIS.**— The female of this species is similar to *D. baxiantaiensis* by having the looped copulatory ducts and broad, long spermathecae but can be distinguished by the small atrium, the presence of two copulatory duct loops, and the anteriorly situated spermathecal heads (Figs. 51A–B).

**DESCRIPTION.**— Described by Schenkel (1963). Cheliceral promargin with three teeth, retromargin with two. Female with epigynal teeth small; atrium small; copulatory ducts long, originating posteriorly, with two loops around spermathecae; spermathecal heads small, situated ventrally on anterior spermathecae; spermathecal bases broad, widely separated; spermathecal stalks broad, anteriorly converging (Figs. 51A–B). Male unknown.

**DISTRIBUTION.**— China (Gansu) (Map 16).

**MATERIAL EXAMINED.**— CHINA: **Gansu**: Kloster Dschoni (Choni), June 8, 1885, female holotype (MNHN).

***Draconarius pseudobrunneus* Wang, sp. nov.**

Figure 52A–B; Map 18

**TYPES.**— Female holotype and 3 female paratypes from Danzhu He drainage, 13.5 air km

SSW of Gongshan, 2700m, N27.631°/E98.621°, Gongshan Co., Nujiang, Yunnan, China (June 30–July 5, 2000; D. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, H.M. Yan, and D.Z. Dong), deposited in HBI (holotype female and 1 paratype female) and CAS (2 paratype females).

**ETYMOLOGY.**— The specific name refers to its similarity to *D. brunneus*.

**DIAGNOSIS.**— The female of this species is similar to *D. parabrunneus* in lacking the epigynal teeth, and having small, broad spermathecae but can be distinguished by the medially situated spermathecal heads and the moderately expanded spermathecal bases (same width as stalks) (Figs. 52A–B).

**FEMALE.**— Total length 7.28. Carapace 3.38 long, 2.08 wide. Abdomen 3.90 long, 2.73 wide. Eye sizes and interdistances: AME 0.09, ALE 0.18, PME 0.15, PLE 0.17; AME–AME 0.09, AME–ALE 0.05, PME–PME 0.10, PME–PLE 0.15, AME–PME 0.13. Leg measurements: I: 7.72 (2.31, 2.60, 1.64, 1.17); II: 7.26 (2.08, 2.55, 1.59, 1.04); III: 6.79 (1.87, 2.24, 1.69, 0.99); IV: 9.81 (2.42, 3.07, 2.47, 1.22). Promargin of chelicera with three teeth, retromargin with two. Epigynal teeth absent; atrium small; epigynum wrinkled on anterior atrium; copulatory ducts small, situated mesad of spermathecae; spermathecal heads small, situated medially on spermathecae; spermathecal bases broad, widely separated; spermathecal stalks widely separated, slightly converging anteriorly (Figs. 52A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 18).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius pseudocapitulatus* Wang, sp. nov.**

Figures 53A–B; Map 19

**TYPES.**— Female holotype and 1 female paratype from Danzhu He drainage, 13.5 air km SSW of Gongshan, 2700m, N27.631°/E98.621°, Gongshan Co., Nujiang, Yunnan, China (June 30 – July 5, 2000; D. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, H.M. Yan, and D.Z. Dong), deposited in HBI; 1 female paratype from Nujiang State Nature Reserve, No. 12 Bridge Camp area, 16.3 air km W of Gongshan, N27.715°/E98.502°, 2775m, Nujiang Prefecture, Gaoligong Shan, Yunnan, China (July 15–19, 2000; H.M. Yan, D. Kavanaugh, C.E. Griswold, H.B. Liang, D. Ubick, and D. Z. Dong), deposited in CAS.

**ETYMOLOGY.**— The specific name refers to its similarity to *D. capitulatus*.

**DIAGNOSIS.**— The female of this species is similar to *D. capitulatus* but can be distinguished by the anteriorly expanded, widely separated spermathecae (fig. 53A–B).

**FEMALE.**— Total length 11.7. Carapace 5.20 long, 3.54 wide. Abdomen 6.50 long, 4.94 wide. Eye sizes and interdistances: AME 0.15, ALE 0.23, PME 0.20, PLE 0.22; AME–AME 0.14, AME–ALE 0.11, PME–PME 0.19, PME–PLE 0.29, AME–PME 0.20. Leg measurements: I: 12.0 (3.64, 3.90, 2.76, 1.69); II: 11.7 (3.25, 4.50, 2.47, 1.46); III: 9.60 (2.73, 3.15, 2.42, 1.30); IV: 13.2 (3.64, 4.42, 3.51, 1.61). Promargin of chelicera with three teeth, retromargin with two. Epigynal teeth absent; atrium broad, near epigastric furrow; copulatory ducts short, situated mesad of spermathecae; spermathecal heads situated anteriorly, mesad of spermathecae; spermathecal bases broad, widely separated; spermathecal stalks short, expanded anteriorly (Figs. 53A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 19).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius pseudowuermlii* Wang, sp. nov.**

Figures 54A–B; Map 18

**TYPES.**— Female holotype from Pass over Gaoligongshan at 2300 m, Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, Baoshan, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI.

**ETYMOLOGY.**— The specific name refers to its similarity to *D. wuermlii*.

**DIAGNOSIS.**— The female of this new species is similar to *D. wuermlii* but can be distinguished by the medially situated, not looped copulatory ducts and the broad, rounded spermathecal bases (fig. 54A–B).

**FEMALE.**— Total length 6.30. Carapace 3.10 long, 2.20 wide. Abdomen 3.20 long, 2.40 wide. Eye sizes and interdistances: AME 0.10, ALE 0.18, PME 0.18, PLE 0.20; AME–AME 0.05, AME–ALE 0.08, PME–PME 0.04, PME–PLE 0.13, AME–PME 0.12. Leg measurements: I: 7.44 (2.24, 2.56, 1.66, 0.98); II: 6.38 (1.96, 2.16, 1.46, 0.80); III: 5.32 (1.56, 1.80, 1.28, 0.68); IV: 7.64 (2.24, 2.64, 1.92, 0.84). Promargin of chelicera with three teeth, retromargin with two. Epigynal teeth short, situated laterad of atrium; atrium broad, with less sclerotized, whitish median piece; copulatory ducts broad, anteriorly extending, situated mesad of spermathecae, connected to spermathecae laterally; spermathecal heads large, widely separated; spermathecal bases broad, rounded; spermathecal stalks long, strongly convoluted (Figs. 54A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 18).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius qingzangensis* (Hu, 2001), NEW COMBINATION**

Map 17

*Coelotes qingzangensis* Hu, 2001:143, figs. 8–54:1–2 (female holotype, 2 female paratypes from Nangqian, Qinghai, China, in SDU, not examined).

**DIAGNOSIS.**— The female is similar to *D. linzhiensis* by the similar spermathecal tubes but can be distinguished by the not separated atria and the strongly expanded anterior spermathecae (larger than stalks).

**DESCRIPTION.**— See Hu (2001). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth situated laterad of atrium, near atrial lateral margins; atrium large; spermathecal heads situated medially on spermathecae; spermathecal bases widely separated; spermathecal stalks broad, anteriorly expanded and converging. Male unknown.

**DISTRIBUTION.**— China (Qinghai) (Map 17).

**MATERIAL EXAMINED.**— None.

***Draconarius quadratus* (Wang et al., 1990), NEW COMBINATION**

Figures 55A–B; Map 17

*Coelotes quadratus* Wang et al., 1990:197, figs. 46–47 (female holotype from Damingshan, Guangxi, China, in HBI, examined).— Song, Zhu and Chen, 1999:377, figs. 224H–I.

**DIAGNOSIS.**— The female of this species is similar to *D. pervicax* but can be distinguished by the widely separated spermathecal bases and the posteriorly situated epigynal hoods (Fig. 55A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth small, situated near atrium; atrium small; epigynal hoods



situated posteriorly near epigastric furrow; copulatory ducts small; spermathecal heads anteriorly situated; spermathecal bases widely separated, broad; spermathecal stalks broad, anteriorly diverging (Figs. 55A–B). Male unknown.

**DISTRIBUTION.**— China (Guangxi) (Map 17).

**MATERIAL EXAMINED.**— CHINA: **Guangxi:** Damingshan, August 10, 1982, female holotype (J.F. Wang, HBI).

***Draconarius rotundus* Wang, sp. nov.**

Figures 56A–B; Map 17

**TYPES.**— Female holotype from Pass over Gaoligongshan at 2300 m, Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, Baoshan, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI.

**ETYMOLOGY.**— The specific name refers to the rounded copulatory ducts.

**DIAGNOSIS.**— The female of this new species can be easily recognized by the posteriorly situated epigynal hoods, the anteriorly expanded copulatory ducts, and the looped, widely separated spermathecae (Figs. 56A–B).

**FEMALE.**— Total length 8.00. Carapace 3.80 long, 2.60 wide. Abdomen 4.20 long, 2.80 wide. Eye sizes and interdistances: AME 0.12, ALE 0.18, PME 0.19, PLE 0.19; AME-AME 0.09, AME-ALE 0.10, PME-PME 0.05, PME-PLA 0.20, AME-PME 0.16. Leg measurements: I: 8.78 (2.62, 3.00, 1.92, 1.24); II: 8.24 (2.42, 2.90, 1.76, 1.16); III: 6.74 (1.96, 2.18, 1.60, 1.00); IV: 10.6 (2.80, 3.38, 3.30, 1.16). Promargin of chelicera with three teeth, retromargin with two. Epigynal teeth short, situated laterally, slightly anterad of atrium; atrium broad; epigynal hoods situated posteriorly laterad of atrium; copulatory ducts broad, originating posteriorly, mesad of spermathecae, extending anteriorly and connected to spermathecae laterally; spermathecal heads situated laterally; spermathecal bases broad, widely separated; spermathecal stalks broad, looped (Figs. 56A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 17).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius rufulus* (Wang et al., 1990), NEW COMBINATION**

Figures 57A–E; 96I; Map 18

*Coelotes rufulus* Wang et al., 1990:194, figs. 41–45 (2 male and 2 female types, holotype not indicated, from Tianmushan, Zhejiang, China, in HBI, examined).— Song, Zhu and Chen, 1999:377, figs. 224L–M, 226S, 228A.

*Coelotes rufuloides* Zhang, Peng and Kim, 1997:295, figs. 8–9 (female holotype from Tiantong Mt., Zhejiang, China, in HBI, examined). **NEW SYNONYMY.**

**DIAGNOSIS.**— This species can be easily recognized by the absence of epigynal teeth, the tongue-like posterior epigynal extension, the elongated, looped copulatory ducts of female (Figs. 57A–B) and by lacking a patellar apophysis, the strongly modified conductor, and the broad, strongly modified embolus of male (Figs. 57C–E).

**DESCRIPTION.**— Described by Wang et al. (1990). Chelicerae with three promarginal and two retromarginal teeth. Female epigynum without epigynal teeth; atrium small, situated posteriorly, near epigastric furrow; copulatory ducts posteriorly originating, extending mesad of spermathecae, and then strongly looped laterad of spermathecae; spermathecal heads small; spermathecal bases widely separated; spermathecal stalks strongly convoluted, anteriorly elongated (Figs. 57A–B).

Male palp without patellar apophysis; RTA long; lateral tibial apophysis large, near RTA; cymbial furrow slightly shorter than half cymbial length; conductor long, broad, posteriorly extending, strongly modified with broad dorsal edge and a strong tooth, with small basal lamella; conductor dorsal apophysis small; embolus long, broad, strongly modified, posterior in origin; median apophysis spoon-like, elongated (Figs. 57C–E).

**DISTRIBUTION.**— China (Anhui, Zhejiang) (Map 18).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang:** Tianmushan, October 15, 1974, 2 male and 2 female paratypes (J.F. Wang, HBI); Tiantong Mt., January 22, 1988, female holotype of *Coelotes rufuloides* (Y.J. Zhang, HBI); Beihai Hotel (no provinces on label), October 29, 1974, 2 females (C. D. Zhu, NBUMS, 74–1990).

### *Draconarius schenkeli* (Brignoli, 1978)

Figures 58A–B; Map 18

*Coelotes schenkeli* Brignoli, 1978: 46, figs. 23–24 (female holotype from Chimakothi, Bhutan, in NHMB, examined).

*Draconarius schenkeli*: Wang, 2002:69.

**DIAGNOSIS.**— The female of this species can be easily identified by the closely situated epigynal teeth, the posteriorly situated epigynal hoods, the long, anteriorly extending copulatory ducts, and the laterally situated spermathecal heads (Figs. 58A–B).

**DESCRIPTION.**— Described by Brignoli (1978). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth short, situated medially on anterior atrial margin; epigynal hoods situated posteriorly, laterad of atrium; copulatory ducts strongly extending and converging anteriorly; spermathecal heads small, laterally situated; spermathecal bases small, slightly separated; spermathecal stalks short, slightly extending laterally (Figs. 58A–B). Male unknown.

**DISTRIBUTION.**— Bhutan (Map 18).

**MATERIAL EXAMINED.**— BHUTAN: Chimakothi, 1900–2300 m, May 22, 1972, female holotype (NHMB, 2305a).

### *Draconarius simplicidens* Wang, sp. nov.

Figures 59A–B; Map 19

**TYPES.**— Female holotype from Pass over Gaoligongshan at 2300 m, Luoshuidong, 28 air km E TengChong, 24°57'N, 98°45'E, native forest, Baoshan, Yunnan, China (October 26–31, 1998; C. Griswold, D. Kavanaugh, C-L. Long), deposited in HBI.

**ETYMOLOGY.**— The specific name refers to the simple epigynum.

**DIAGNOSIS.**— The female of this new species is similar to *D. dubius* and *D. patellabifidus* by lacking epigynal teeth and having broad spermathecae but can be recognized by the medially situated spermathecal heads (Figs. 59A–B).

**FEMALE.**— Total length 8.00. Carapace 3.80 long, 2.20 wide. Abdomen 4.20 long, 2.80 wide. Eye sizes and interdistances: AME 0.10, ALE 0.18, PME 0.18, PLE 0.20; AME–AME 0.05, AME–ALE 0.05, PME–PME 0.10, PME–PLE 0.11, AME–PME 0.11. Leg measurements: I: 7.70 (2.42, 2.78, 1.60, 0.90); II: 6.58 (2.02, 2.34, 1.42, 0.80); III: 5.08 (1.58, 1.66, 1.14, 0.70); IV: 7.26 (2.32, 2.60, 1.64, 0.70). Promargin of chelicera with three, retromargin with two to three teeth. Epigynal teeth absent; atrium small, indistinct; copulatory ducts small, originating posteriorly, extending mesad of spermathecae; spermathecal heads large, situated mesad of spermathecae; spermathecal bases broad, widely separated; spermathecal stalks broad, anteriorly diverging (Figs. 59A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Yunnan) (Map 19).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius singulatus* (Wang et al., 1990)**

Figures 60A–E; Map 19

*Coelotes singulatus* Wang et al., 1990:192, figs. 36–40 (1 male and 2 female types, holotype not indicated, from Nanshanping, Chenbu, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:378, figs. 224R–S, 227A, 228D.

*Draconarius singulatus* Wang, 2002:69.

**DIAGNOSIS.**— The female of this species is similar to *D. gorkha* but can be distinguished by the broad, medially situated copulatory ducts (Figs. 60A–B). The male is similar to *D. everesti* by the short cymbial furrow and the prolaterally originating embolus but can be distinguished by the long RTA and the distinct lateral tibial apophysis (Figs. 60C–E).

**DESCRIPTION.**— Described by Wang et al. (1990). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth short, situated slightly anterior atrial margin; atrium small; copulatory ducts broad, situated mesad of spermathecae; spermathecal heads not visible from dorsal view; spermathecae broad, widely separated (Figs. 60A–B). Male palpal patellar apophysis present, long; RTA slightly longer than half tibial length; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor broad, with small basal lamella; conductor dorsal apophysis slender; embolus prolateral in origin; median apophysis elongated, spoon-like (Figs. 60C–E).

**DISTRIBUTION.**— China (Hunan) (Map 19).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Chanbu, Nanshanping, July 30, 1982, 1 male and 2 female types (J. F. Wang, HBI).

***Draconarius stemmleri* (Brignoli, 1978)**

Figures 61A–B; Map 19

*Coelotes stemmleri* Brignoli, 1978:43, figs. 15–16 (female holotype from Sha Gogona, Bhutan, in NHMB, female paratype from Gogona, Kotota, Bhutan, in MCV, examined).

*Draconarius stemmleri*: Wang, 2002:69.

**DIAGNOSIS.**— The female of this species is similar to *D. yadongensis* but can be distinguished by the medially situated spermathecal heads (Figs. 61A–B).

**DESCRIPTION.**— Described by Brignoli (1978). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth short, broad, situated slightly anterior atrial margin; atrium small; copulatory ducts small, situated mesad of spermathecae; spermathecal heads large, situated mesad of spermathecae; spermathecal bases broad, widely separated; spermathecal stalks broad, strongly expanded anteriorly (Figs. 61A–B). Male unknown.

**DISTRIBUTION.**— Bhutan (Map 19).

**MATERIAL EXAMINED.**— BHUTAN: Sha Gogona, 3100 m, July–August, 1972, female holotype (NHMB, 2303a). Kotoka, Gogona, 2600–3400 m alt., June 10, 1972, 1 female paratype (MCV).

***Draconarius streptus* (Zhu and Wang, 1994), NEW COMBINATION**

Map 20

*Coelotes streptus* Zhu and Wang, 1994:40, figs. 13–14 (female holotype from Kangding, Sichuan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:378, figs. 224V–W.

**DIAGNOSIS.**— The female of this species is similar to *D. syzygiatus* in lacking epigynal teeth, having broad atrium and medially extending spermathecal bases but can be distinguished by the long, slender, anteriorly converging spermathecal stalks.

**DESCRIPTION.**— Described by Zhu and Wang (1994). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth absent; atrium large; spermathecal heads small, situated anteriorly; spermathecal bases widely separated, medially extending; spermathecal stalks slender, laterally extending, anteriorly converging and close together. Male unknown.

**DISTRIBUTION.**— China (Sichuan) (Map 20).

**MATERIAL EXAMINED.**— None.

***Draconarius striolatus* (Wang et al., 1990)**

Figure 62A–B; Map 20

*Coelotes striolatus* Wang et al., 1990:190, figs. 34–35 (female holotype from Yuzhong, Gansu, China, in HBI, examined).— Song, Zhu and Chen, 1999:378, figs. 225A–B.

*Draconarius striolatus*: Wang, 2002:69.

**DIAGNOSIS.**— The female of this species is similar to *D. stemmleri* but can be distinguished by the absence of epigynal teeth (Figs. 62A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth absent; atrium large; copulatory ducts small, situated posteriorly mesad of spermathecae; spermathecal heads long, situated mesad of spermathecae; spermathecal bases broad, widely separated; spermathecal stalks anteriorly expanded and converging (Figs. 62A–B). Male unknown.

**DISTRIBUTION.**— China (Gansu) (Fig. Map 20).

**MATERIAL EXAMINED.**— CHINA: **Gansu**: Yuzhong, August 16, 1988, female holotype (J.F. Wang, HBI).

***Draconarius strophadatus* (Zhu and Wang, 1991), NEW COMBINATION**

Map 20

*Coelotes strophadatus* Zhu and Wang, 1991:3, figs. 12–13 (female holotype from Huangshan, Anhui, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:378, figs. 225C–D.

**DIAGNOSIS.**— The female of this species is similar to *D. huizhunesis* by having the long epigynal teeth but can be distinguished by the closely situated spermathecal stalks and widely separated spermathecal heads.

**DESCRIPTION.**— See Zhu and Wang (1991). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth situated anteriorly and close together, strongly elongated; spermathecal bases small, slightly separated; spermathecal stalks close together, convoluted, and anteriorly diverging. Male unknown.

**DISTRIBUTION.**— China (Anhui) (Map 20).

**MATERIAL EXAMINED.**— None.

***Draconarius subtitanus* (Hu, 1992), New Combination**

Map 20

*Tegenaria pagana*: Hu and Li, 1987:283, figs. 20.3–4 (misidentification).*Coelotes subtitanus* Hu, 1992:42, figs. 9–10 (female holotype, 2 female paratypes from Yadong, Tibet, China, in SDU, not examined).— Hu. 2001:147, figs. 8–57.1–2.

**DIAGNOSIS.**— The female is similar to *D. himalayaensis* and *D. altissimus* in having the short epigynal teeth, anteriorly situated spermathecal heads and rounded, closely situated spermathecae but can be distinguished from *D. himalayaensis* by the epigynal teeth position (close to atrium), from *D. altissimus* by the slightly separated spermathecae.

**DESCRIPTION.**— See Hu (1992). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth short, widely separated, situated near anterior atrium; atrium broad, posteriorly situated; spermathecal heads situated anteriorly; spermathecal bases widely separated; spermathecal stalks broad, rounded, slightly separated. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 20).

**MATERIAL EXAMINED.**— None.

***Draconarius syzygiatus* (Zhu and Wang, 1994), NEW COMBINATION**

Map 21

*Coelotes syzygiatus* Zhu and Wang, 1994:37, figs. 1–4 (female holotype and male paratype from Emei Mt., Sichuan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:378, figs. 225G–H, 227C, 228F.

**DIAGNOSIS.**— The female of this species is similar to *D. streptus* by the absence of epigynal teeth, the presence of broad atrium, and the medially extending spermathecal bases but can be distinguished by the strongly spiraled, rounded spermathecal stalks. The male can be easily identified by the long, posteriorly extending conductor.

**DESCRIPTION.**— See Zhu and Wang (1994). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth absent; atrium large; spermathecal heads small, situated anteriorly; spermathecal bases widely separated, medially extending; spermathecal stalks long, spiraled, rounded. Male palpal patellar apophysis small; RTA short; lateral tibial apophysis long, slender; cymbial furrow about half cymbial length; conductor strongly elongate (about the cymbial length), posteriorly extended and looped, with broad base and slender apex; conductor lamella small; conductor dorsal apophysis present; embolic base small; embolus long, slender, strongly extended posteriorly and then curved back anteriorly; median apophysis small, spoon-like.

**DISTRIBUTION.**— China (Sichuan)(Map 21).

**MATERIAL EXAMINED.**— None.

***Draconarius terebratus* (Peng and Wang, 1997), NEW COMBINATION**

Figures 63A–E; 96G–H; Map 21

*Coelotes terebratus* Peng and Wang, 1997:330, figs. 27–31. (female holotype and male allotype from Tianpingshan, Sangzhi, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:378, figs. 225M–N, 227E, 228H.

**DIAGNOSIS.**— The female of this species is similar to *D. ornatus* by lacking epigynal teeth, having posteriorly situated epigynal hoods, anteriorly extending copulatory ducts, and long spermathecal heads but can be distinguished by the rounded atrium and the broad spermathecal bases

(Figs. 63A–B). The male can be recognized by the large lateral tibial apophysis, the lobed embolic base, and the long, toothed embolus (Figs. 63C–E).

**DESCRIPTION.**— Described by Peng and Wang (1997). Promargin of chelicera with three teeth, retromargin with two. Female lacking epigynal teeth; atrium large; epigynal hoods situated posteriorly laterad of atrium; copulatory ducts posteriorly originating, strongly expanded anteriorly; spermathecal heads long, slender, anteriorly extending; spermathecal bases small, widely separated; spermathecal stalks anteriorly diverging (Figs. 63A–B). Male palpal patellar apophysis present; RTA long; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor long, broad, with slender, posteriorly hooked apex and small basal lamella; conductor dorsal apophysis small; embolic base lobed; embolus posterior in origin, modified with a small tooth; median apophysis small, spoon-like (Figs. 63C–E).

**DISTRIBUTION.**— China (Hunan) (Map 21).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Sangzhi, Tianpingshan, October 16, 1986, female holotype and male allotype (J.F. Wang, HBI).

*Draconarius tibetensis* Wang, sp. nov.

Figures 64A–C; Map 21

**TYPE.**— Male holotype from Yupik Valley, 29.48°N, 96.14°E, Tibet, China (May 14, 1998; G. Schaller), deposited in AMNH.

**ETYMOLOGY.**— The specific name refers to the type locality.

**DIAGNOSIS.**— The male of this species is similar to *D. baronii* but can be distinguished by the broad dorsal edge of conductor (Figs. 64A–C).

**MALE.**— Total length 11.2. Carapace 6.80 long, 3.40 wide. Abdomen 4.40 long, 3.20 wide. Eye sizes and interdistances: AME 0.14, ALE 0.20, PME 0.15, PLE 0.17; AME-AME 0.14, AME-ALE 0.14, PME-PME 0.28, PME-PLE 0.30, AME-PME 0.18. Leg measurements: I: 16.8 (4.20, 5.60, 4.40, 2.60); II: 15.6 (4.00, 5.60, 4.20, 2.40); III: 14.2 (3.60, 4.40, 4.00, 2.20); IV: — (4.40, —, —, —). Chelicerae with three promarginal, and two widely separated retromarginal teeth. Male palp with large patellar apophysis; RTA slightly longer than half tibial length; lateral tibial apophysis widely separated from RTA; cymbial furrow short; conductor short, with broad dorsal edge; conductor dorsal apophysis small; conductor lamella large; embolus posterior in origin; median apophysis spoon-like, elongated (Figs. 64A–C).

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Tibet) (Map 21).

**OTHER MATERIAL EXAMINED.**— None.

*Draconarius trifasciatus* (Wang and Zhu, 1991)

Map 22

*Coelotes trifasciatus* Wang and Zhu, 1991:3, figs.1–4 (female holotype and male paratype from Mt. Emei, Sichuan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:388, figs. 225U–V, 227I, 228J. *Draconarius trifasciatus*: Wang, 2002:69.

**DIAGNOSIS.**— The female of this species is similar to *D. stemmleri* but can be distinguished by the less distinct spermathecal heads and the anteriorly converging spermathecae. The male can be recognized by the large cymbial furrow, the long conductor, and the toothed (lobed) embolic base.

**DESCRIPTION.**— See Wang and Zhu (1991). Chelicerae with three promarginal, and two retro-marginal teeth. Female epigynum with widely separated, posteriorly situated, broad epigynal teeth; atrium broad, situated posteriorly near epgastric furrow; spermathecae broad. Male palp with patellar apophysis; RTA long; lateral tibial apophysis situated near RTA; cymbial furrow large, almost as long as cymbium; conductor long, slender; conductor dorsal apophysis present; embolic base with a prolateral lobe; embolus long, posterior in origin.

**DISTRIBUTION.**— China (Sichuan) (Map 22).

**MATERIAL EXAMINED.**— None.

***Draconarius tryblionatus* (Wang and Zhu, 1991), NEW COMBINATION**

Map 21

*Coelotes tryblionatus* Wang and Zhu, 1991:3, figs. 5–8 (female holotype, male and female paratypes from Mt. Qingcheng, Sichuan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:388, figs. 226C–D, 227K, 228L.

**DIAGNOSIS.**— The female of this species is similar to *D. streptus* and *D. syzygiatus* in lacking epigynal teeth and having broad atrium but can be distinguished by the laterally extending spermathecal bases. The male is similar to *D. uncinatus* in having the bifurcate patellar apophysis, a broad conductor, and a strong embolus but can be distinguished by the spiraled embolus and the broad median apophysis.

**DESCRIPTION.**— See Wang and Zhu (1991). Chelicerae with three promarginal, and three retromarginal teeth. Female without epigynal teeth; atrium large; spermathecal bases widely separated, laterally extending; spermathecal stalks laterally extending and then curved medially, anteriorly converging and close together. Male palp with bifurcate patellar apophysis; RTA long; lateral tibial apophysis present; cymbial furrow short; conductor broad; median apophysis situated near conductor; embolus strong, spiraled.

**DISTRIBUTION.**— China (Sichuan) (Map 21).

**MATERIAL EXAMINED.**— None.

***Draconarius uncinatus* (Wang et al., 1990), NEW COMBINATION**

Figures 65A–C; 96F; Map 22

*Coelotes uncinatus* Wang et al., 1990:188, figs. 29–31 (2 male types, holotype not indicated, from Tianmushan, Zhejiang, China, in HBI, examined).— Song, Zhu and Chen, 1999:388, figs. 227L, 228M.

**DIAGNOSIS.**— This species is similar to *D. tryblionatus* in having a bifurcate patellar apophysis, a broad conductor, and a strong embolus but can be distinguished by the non-spiraled embolus and the small median apophysis (Fig. 65A–C).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retromargin with two. Male palp with bifurcate patellar apophysis; RTA long; lateral tibial apophysis present; cymbial furrow short; conductor broad; conductor dorsal apophysis small; conductor lamella small; embolus posterior in origin, broad; median apophysis spoon-like, small (Figs. 65A–C). Female unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 22).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang:** Tianmushan, October 15, 1974, 2 male types (J.F. Wang, HBI).

***Draconarius venustus* Ovtchinnikov, 1999**

Map 22

*Draconarius venustus* Ovtchinnikov, 1999:70, figs. 23–27 (male holotype and female paratype from Khszratisho Mt., Yachsriver Valley, Tajikistan, deposited in cSO, not examined).— Wang, 2000:69.

**DIAGNOSIS.**— Similar to *D. wudangensis* in having the medially situated and widely separated epigynal teeth, and similar spermathecal tubes but can be distinguished by the posteriorly situated spermathecal heads and the strong anterior expansion of spermathecae of female, and by the long RTA (almost tibial length), short tibia (about patellar length), and the short patellar apophysis of male.

**DESCRIPTION.**— See Ovtchinnikov (1999). Chelicerae with three promarginal, and two retro-marginal teeth. Female epigynal teeth short, widely separated; atrium small, situated posteriorly near epigastric furrow; copulatory ducts apparent, originating posteriorly mesad of spermathecae; spermathecal heads situated posteriorly, near spermathecal bases; spermathecal bases widely separated; spermathecal stalks strongly converging and expanded anteriorly. Male palp with patellar apophysis small; RTA almost as long as tibia; lateral tibial apophysis present; cymbial furrow almost as long as cymbium; conductor short, with large lamella; conductor dorsal apophysis present; embolus posterior in origin, long; median apophysis spoon-like.

**DISTRIBUTION.**— Tajikistan (Map 22).

**MATERIAL EXAMINED.**— None.

***Draconarius wenzhouensis* (Chen, 1984)**

Figures 66A–B; Map 22

*Coelotes wenzhouensis* Chen, 1984:3, figs. 7–8 (female holotype and 1 female paratype from Xueshan, Wenzhou, Zhejiang, China, in HTC, examined).— Chen and Zhang, 1991:190, figs. 189.1–2;— Song, Zhu and Chen, 1999:388, figs. 226I–J.

*Draconarius wenzhouensis*: Wang, 2002:69.

**DIAGNOSIS.**— This species is similar to *D. labiatus* but can be distinguished by the large spermathecal heads and the anteriorly extending spermathecae (Fig. 66A–B).

**DESCRIPTION.**— Described by Chen (1984). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth short, close together, anteriorly situated; atrium situated posteriorly near epigastric furrow, with anterior atrial margin lip-shaped and expanded posteriorly; copulatory ducts posteriorly originating, extending mesad of spermathecae; spermathecal heads large; spermathecal bases widely separated; spermathecal stalks strongly expanded and converging anteriorly (Figs. 66A–B). Male unknown.

**DISTRIBUTION.**— China (Zhejiang) (Map 22).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang**: Wenzhou, Xueshan, March 10–12, 1980, female holotype and 2 female paratypes (Z.F. Chen, HTC).

***Draconarius wudangensis* (Chen and Zhao, 1997)**

Figures 67A–E; Map 23

*Coelotes wudangensis* Chen and Zhao, 1997:87, figs. 1–4 (1 male and 1 female paratypes, holotype not indicated, from Jinding, Wudangshan, Hubei, China, in HUW, examined).— Song, Zhu and Chen, 1999:388, figs. 226K–L, 227O, 229A.

*Draconarius wudangensis*: Wang, 2002:69.

*Draconarius parawudangensis* Zhang, Zhu and Song, 2002:53, figs. 5–6. NEW SYNONYMY.



**DIAGNOSIS.**— The female is similar to *D. aspinatus*, *D. calcariformis*, *D. coreanus*, *D. davidi*, *D. linzhiensis*, *D. picta*, *D. qingzangensis*, and *D. venustus* in having similar spermathecae but can be distinguished by the medially situated, widely separated (widely separated from atrium) epigynal teeth, the anteriorly situated (anterior 1/3 of spermathecae) spermathecal heads, and the broad spermathecal bases (Figs. 67A–B). The male is similar to *D. venustus* but can be distinguished by the short RTA (half tibial length), long tibia (twice patellar length), and the long patellar apophysis (Figs. 67C–E).

**DESCRIPTION.**— Described by Chen and Zhao (1997) and Wang (2002). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth short, widely separated; atrium small, situated posteriorly near epigastric furrow; copulatory ducts originating posteriorly, extending mesad of spermathecae; spermathecal heads situated anteriorly; spermathecal bases widely separated, broad; spermathecal stalks broad, anteriorly extending and converging (Figs. 67A–B). Male palp with patellar apophysis long; RTA approximately half tibial length; lateral tibial apophysis present; cymbial furrow long, slightly more than half cymbial length; conductor short, with large basal lamella; conductor dorsal apophysis present; embolus posterior in origin, long; median apophysis spoon-like, elongated (Figs. 67C–E).

**DISTRIBUTION.**— China (Hubei, Shaanxi, Shanxi) (Map 23).

**MATERIAL EXAMINED.**— CHINA: **Hubei:** Wudangshan, Jinding, August 1996, 1 male and 1 female paratypes (J. Chen, HUW); Wudangshan, Jinding, September 24, 1997, 7 females (X.P. Wang, IZB); Wudangshan, Nanya to Jinding, September 24, 1997, 1 male and 16 females (X.P. Wang, IZB). **Shaanxi:** Taibaishan, Haoping, August 11, 1989, 1 male and 1 female, 1 male and 1 female / 1 male and 1 female, 1 male (X.P. Wang, AMNH and MCB); Taibaishan, Mingxinshi, Aug. 8, 1989, 1 female (X.P. Wang, IZB). **Shanxi:** Yongji, July 20, 1980, 1 female (M.S. Zhu, HUB, No-044).

### *Draconarius wuermlii* (Brignoli, 1978)

Figures 68A–B; Map 23

*Coelotes wuermlii* Brignoli, 1978:44, figs. 21–22 (female holotype from Dechhi Paka, Bhutan, in NHMB, examined).

*Paracoelotes wuermlii*: Brignoli, 1982:349.

*Draconarius wuermlii*: Wang, 2002:69.

**DIAGNOSIS.**— The female of this species is similar to *D. pseudowuermlii* but can be distinguished by the looped copulatory ducts, the less convoluted spermathecae, and the small spermathecal bases (Figs. 68A–B).

**DESCRIPTION.**— Described by Brignoli (1978). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth short, widely separated, situated posteriorly and laterad of atrium; atrium small; copulatory ducts originating posteriorly and mesad of spermathecae, looped around spermathecae; spermathecal heads situated anteriorly; spermathecal bases widely separated; spermathecal stalks long, anteriorly converging (Figs. 68A–B). Male unknown.

**DISTRIBUTION.**— Bhutan (Map 23).

**MATERIAL EXAMINED.**— BHUTAN: Dechhi Paka, 3300 m, June 20, 1972, female holotype (Basel-Bhutan Expedition 1972, NHMB, 2304a).

***Draconarius yadongensis* (Hu and Li, 1987), NEW COMBINATION**

Map 23

*Wadotes yadongensis* Hu and Li, 1987:280, figs. 20.1–2 (female holotype from Yadong, Tibet, China, in SDU, not examined).— Song, Zhu and Chen, 1999:395, figs. 230M–N;— Hu, 2001:153, figs. 8–61.1–2.

*Coelotes yadongensis*: Hu, 1992:43.

**DIAGNOSIS.**— The female of this species is similar to *D. stemmleri* but can be distinguished by the anteriorly situated spermathecal heads.

**DESCRIPTION.**— See Hu and Li (1987). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth short, broad, situated slightly anterior of atrial margin; atrium small; spermathecal bases broad, widely separated; spermathecal stalks broad, strongly expanded anteriorly. Male unknown.

**DISTRIBUTION.**— China (Tibet) (Map 23).

**MATERIAL EXAMINED.**— None.

***Draconarius yichengensis* Wang, sp. nov.**

Figures 69A–B; Map 23

**TYPES.**— Female holotype from Yicheng, Shanxi, China (August 15, 1983; M.S. Zhu), deposited in HUB (No-83-0025).

**ETYMOLOGY.**— The specific name refers to the type locality.

**DIAGNOSIS.**— The female of this new species can be easily recognized by the long epigynal teeth, the broad, rounded spermathecae, and the ventrally originating spermathecal heads (Figs. 69A–B).

**FEMALE.**— Total length 6.20. Carapace 3.12 long, 2.05 wide. Abdomen 3.08 long, 1.81 wide. Eye sizes and interdistances: AME 0.08, ALE 0.15, PME 0.11, PLE 0.12; AME-AME 0.09, AME-ALE 0.15, PME-PME 0.13, PME-PLE 0.16. Leg measurements: I: 7.94 (2.24, 2.81, 1.72, 1.17); II: 7.43 (2.10, 2.54, 1.65, 1.14); III: 7.06 (1.95, 2.32, 1.73, 0.94); IV: 9.57 (2.56, 3.11, 2.70, 1.20). Promargin of chelicera with three teeth, retromargin with two. Female epigynal teeth long, situated near anterior atrial margin; atrium broad; copulatory ducts small; spermathecal heads anteriorly situated, originating ventrally; spermathecal bases broad, widely separated; spermathecal stalks broad, rounded, anteriorly converging (Figs. 69A–B). Male unknown.

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Shanxi) (Map 23).

**OTHER MATERIAL EXAMINED.**— None.

***Draconarius yosiianus* (Nishikawa, 1999)**

Map 24

*Coelotes yosiianus* Nishikawa, 1999:23, figs. 1–5 (female holotype and 1 female paratype from Jiabao Dong, Xingren Cun, Jiazhuang Xiang, Bama Xian, Guangxi, China, in NSMT, not examined).

*Draconarius yosiianus*: Wang, 2002:69.

**DIAGNOSIS.**— The female of this species can be easily recognized by the absence of eyes, the widely separated, medially expanded spermathecae.

**DESCRIPTION.**— See Nishikawa (1999). Chelicerae with three promarginal, and two retromarginal teeth. Female epigynal teeth short, situated slightly anterior atrium; atrium large; spermathecal bases widely separated; spermathecal stalks widely separated, medially expanded. Male unknown.

**DISTRIBUTION.**— China (Guangxi) (Map 24). Known only from a cave.

**MATERIAL EXAMINED.**— None.

### Genus *Femoracoelotes* Wang, 2002

*Femoracoelotes* Wang, 2002:81 (type species, by original designation, *Coelotes platnicki* Wang and Ono, 1998 from China).

**DIAGNOSIS.**— The female of this genus can be easily recognized by the absence of epigynal teeth and the presence of broad copulatory ducts, the male by the presence of a femoral apophysis and the absence of median apophysis (Figs. 70–71).

**PHYLOGENETIC PLACEMENT.**— The presence of four cheliceral retromargin teeth suggests *Femoracoelotes* is the sister group of *Coronilla* from China, together they form the sister group of all other coelotines (Wang, 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— China (Map 25).

**COMPOSITION.**— 2 species:

1. *Femoracoelotes latus* (Wang, Tso and Wu, 2001)
2. *Femoracoelotes platnicki* (Wang and Ono, 1998)

#### *Femoracoelotes latus* (Wang, Tso and Wu, 2001)

Figures 70A–E; Map 25

*Coelotes latus* Wang, Tso and Wu, 2001:130, figs. 11–21 (male holotype, 1 male and 1 female paratypes from Nantou, Taiwan, in THU, examined).

*Femoracoelotes latus*: Wang, 2002:81.

**DIAGNOSIS.**— This species can be distinguished from *F. platnicki* by the small, slightly expanded copulatory ducts, the less convoluted spermathecae of female (Figs. 70A–B), and by the short conductor and the short, and dorsally situated conductor dorsal apophysis (Figs. 70C–E).

**DESCRIPTION.**— Described by Wang, Tso and Wu (2001). Chelicerae with three promarginal and four retromarginal teeth. Epigynal teeth absent; atria small; copulatory ducts broad, slightly extending anteriorly; spermathecal heads small, anteriorly situated; spermathecal bases broad, widely separated; spermathecal stalks slightly elongated, not convoluted (Figs. 70A–B). Male palp with femoral apophysis slightly bifurcate; femora with numerous short spines on distal prolateral surface; patellar apophysis short; RTA as long as tibia; lateral tibial apophysis absent; cymbial furrow short; conductor short, broad, with small basal lamella; conductor dorsal apophysis short; median apophysis absent; embolus strong, prolateral to posterior in origin, with bifurcate apex (Figs. 70C–E).

**DISTRIBUTION.**— China (Taiwan) (Map 25).

**MATERIAL EXAMINED.**— CHINA: **Taiwan:** Nantou, Hui-Sun Experimental Forest Station, October 1997, male holotype, 1 male and 1 female paratypes (Hai-Ying Wu, THU).

#### *Femoracoelotes platnicki* (Wang and Ono, 1998)

Figures 71A–E; Map 25

*Coelotes platnicki* Wang and Ono, 1998:148, figs. 15–19 (male holotype and female paratype from Mt. Tengchih, Paoshan-tsun, Taoyuan-hsiang, Kaohsiung-hsien, Taiwan, in NSMT, examined).— Song, Zhu and Chen, 1999:377.

*Femoracoelotes platnicki*: Wang, 2002:82, figs. 227–241.

**DIAGNOSIS.**— This species can be distinguished from *F. latus* by the broad, anteriorly expanded copulatory ducts, the convoluted spermathecae of female (Figs. 71A–B), and by the broad, strongly elongated conductor and the long, ventrally situated conductor dorsal apophysis of male (Figs. 71C–E).

**DESCRIPTION.**— Described by Wang and Ono (1998). Chelicerae with three promarginal and four retromarginal teeth (occasionally five). Female epigynal teeth absent; atrium small, situated posteriorly near epigastric furrow; copulatory ducts broad, anteriorly expanded; spermathecal heads large; spermathecal bases widely separated; spermathecal stalks short, convoluted (Figs. 71A–B). Male palp with femoral apophysis bifurcate; femora with numerous short spines on distal prolateral surface; patellar apophysis present; RTA as long as tibia; lateral tibial apophysis absent; cymbial furrow short; conductor long, broad, strongly modified, lamella small, dorsal apophysis long, ventrally situated; median apophysis absent; embolus strong, prolateral to posterior in origin, with slightly modified apex (Figs. 71C–E).

**DISTRIBUTION.**— China (Taiwan) (Map 25).

**MATERIAL EXAMINED.**— CHINA: Taiwan: Kaohsiung-hsien, Taoyuan-hsiang, Paoshan-tsun, Mt. Tengchih, 1550–1800 m alt., November 1, 1989, 5 males and 7 females (H. Ono, NSMT, NSMT-Ar.3421); Kaohsiung-hsien, Taoyuan-hsiang, Paoshan-tsun, Mt. Tengchih, 1550 m alt., November 1, 1989, 1 male (H. Ono, NSMT, NSMT-Ar.3430); Kaohsiung-hsien, Taoyuan-hsiang, Paoshan-tsun, Mt. Tengchih, 1550–1800 m alt., November 1, 1989, male holotype and female paratype (H. Ono, NSMT, NSMT-Ar.3421).

### Genus *Leptocoelotes* Wang, 2002

*Leptocoelotes* Wang, 2002:105 (type species, by original designation, *Coelotes pseudoluniformis* Zhang, Peng and Kim, 1997 from China).

**DIAGNOSIS.**— The female can be easily recognized by the broad, weakly sclerotized epigynal teeth, the shallow atrium, and the short copulatory ducts, and the male by the complex conductor, the absence of a conductor dorsal apophysis, and the absence of a median apophysis (Figs. 72–73).

**PHYLOGENETIC PLACEMENT.**— Remains unresolved with *Tegeocoelotes* and the clade with spoon-like median apophysis and slender epigynal teeth (Wang, 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— China (Map. 26).

**COMPOSITION.**— 2 species:

1. *Leptocoelotes edentulus* (Wang and Ono, 1998)
2. *Leptocoelotes pseudoluniformis* (Zhang, Peng and Kim, 1998)

#### *Leptocoelotes edentulus* (Wang and Ono, 1998)

Figures 72A–B; Map 26

*Coelotes edentulus* Wang and Ono, 1998:142, figs. 1–2 (female holotype from Ilan, Taiwan, in NSMT, examined).— Song, Zhu and Chen, 1999:375.

*Leptocoelotes edentulus*: Wang, 2002:105.

**DIAGNOSIS.**— The female of this species can be distinguished from *L. pseudoluniformis* by the anteriorly situated epigynal hoods and the posteriorly originating copulatory ducts (Figs. 72A–B).

**DESCRIPTION.**— Described by Wang and Ono (1998). Chelicerae with five to six promarginal and five retromarginal teeth. Female epigynal teeth broad but weak, indistinct; atrium broad; epigynal hoods deep, situated anterad of atrium; copulatory ducts short, broad, originating posteriorly

and laterad of spermathecae; spermathecal heads small, situated anteriorly, laterally extending; spermathecal bases broad, slightly separated; spermathecal stalks short, close together (Figs. 72A–B). Male unknown.

**DISTRIBUTION.**— China (Taiwan) (Map 26).

**MATERIAL EXAMINED.**— China: **Taiwan:** Ilan, Tienking-miao, near Tali, 50 m, March 17, 1991, female holotype (H. Ono, NSMT, NSMT-Ar.3427); Nantou, Tatachia, 2100 m, March 5, 1991 1 female paratype (H. Ono, NSMT, NSMT-Ar.3427).

***Leptocoelotes pseudoluniformis* (Zhang, Peng and Kim, 1997)**

Figures 73A–G; Map 26

*Coelotes pseudoluniformis* Zhang, Peng and Kim, 1997:293, fig. 6–7 (female holotype from Tiantong, Zhejiang, China, in HBI, examined).

*Leptocoelotes pseudoluniformis*: Wang, 2002:105.

**DIAGNOSIS.**— The female of this species can be recognized from *L. edentulus* by the laterally situated epigynal hoods and the anteriorly originating copulatory ducts (Figs. 73A–D). The male can be distinguished by the tiny lateral tibial apophysis, the strongly bifurcate conductor, the absence of conductor dorsal apophysis, and the absence of median apophysis (Figs. 73E–G).

**DESCRIPTION.**— Described by Zhang, Peng and Kim (1997). Chelicerae with five promarginal and four to five retromarginal teeth. Female epigynal teeth broad but weak, situated on anterior atrial margin; atrium broad; epigynal hoods deep, situated laterad of atrium; copulatory ducts short, originating anteriorly and laterad of spermathecae; spermathecal heads small, situated anteriorly; spermathecal bases broad, widely separated; spermathecal stalks short, broad, widely separated (Figs. 73A–D). Male palp with patellar apophysis small, dorsally curved; RTA approximately half tibial length; lateral tibial apophysis tiny, situated posteriorly near RTA; cymbial furrow short; conductor strongly bifurcate, slightly spiraled; conductor dorsal apophysis absent, lamella small; embolus posterior in origin; median apophysis absent (Figs. 73E–G).

**DISTRIBUTION.**— China (Zhejiang, Hunan) (Map 26).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang:** Tiantong, January 20, 1988, female holotype (Y.J. Zhang, HBI). **Hunan:** Changsha, Yuelushan, Dec. 22, 1982, 2 males and 4 females (J.F. Wang, HBI).

**Genus *Longicoelotes* Wang, 2002**

*Longicoelotes* Wang, 2002:109 (type species, by original designation, *Longicoelotes karschi* Wang, 2002).

**DIAGNOSIS.**— The female can be easily recognized by the absence of epigynal teeth and the distinct shape of epigynum, and the male by the strongly elongated patellar apophysis and the reduced median apophysis (Figs. 74A–E).

**PHYLOGENETIC PLACEMENT.**— The reduced atrium and the presence of small copulatory ducts support the sister group relationship between *Longicoelotes* and all coelotines with epigynal teeth (Wang 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— China, Senkaku (Map. 27).

**COMPOSITION.**— 3 species, including 2 new combinations:

1. *Longicoelotes karschi* (Wang, 2002)
2. *Longicoelotes kulianganus* (Chamberlin, 1924), NEW COMBINATION
3. *Longicoelotes senkakuensis* (Shimojana, 2000), NEW COMBINATION

***Longicoelotes karschi* Wang, 2002**

Figures 74A–E; Map 27

*Coelotes mollendorffi*: Schenkel, 1963:280, fig. 158.— Chen and Zhang, 1991:187, fig. 185 (misidentification).

*Coelotes moellendorffi*: Song, Zhu and Chen, 1999:376, figs. 221E–F, 222M, 224A (misidentification).

*Longicoelotes karschi* Wang, 2002:109.

**DIAGNOSIS.**— Same as for genus (Figs. 74C–E).

**DESCRIPTION.**— Described by Wang (2002). Chelicerae with three promarginal, two retromarginal teeth. Female without epigynal teeth; middle epigynum relatively elevated with clear lateral edges which converge anteriorly; atrium small; copulatory ducts short, originating and situated laterad of spermathecae; spermathecal heads apparent, extending laterally; spermathecal bases broad, slightly separated; spermathecal stalks short, situated close together (Figs. 74A–B). Male palp with patellar apophysis strongly elongated, longer than tibial length; RTA almost as long as tibia; lateral tibial apophysis widely separated from RTA, situated relatively dorsally; cymbial furrow short; conductor short, broad, with a dorsally bifurcate apophysis and ventrally broad apophysis; conductor lamella small; conductor dorsal apophysis present; median apophysis reduced to a small apophysis, not spoonlike; embolus basal in origin (Figs. 74C–E).

**DISTRIBUTION.**— China (Jiangsu, Zhejiang) (Map 27).

**MATERIAL EXAMINED.**— CHINA: **Zhejiang**: West Tschenkiang, April 1872, 1 female (A. David, MNHN, B2011 bis); Hangtscheou, 1925, 3 females (MNHN, B2011 bis); Lin-An, October 19, 1974, 3 males and 3 females (C.D. Zhu, NBUMS). **Jiangsu**: Nanjin, Zijin (Purple) Mt., 350–450 m, September 13, 1997, male holotype (X.P. Wang, AMNH); Nanjin, Zijin (Purple) Mt., October 9, 1988, 1 female paratype (P. Beron, AMNH).

***Longicoelotes kulianganus* (Chamberlin, 1924), NEW COMBINATION**

Map 27

*Coelotes kulianganus* Chamberlin, 1924:24, fig. 40 (female holotype from Kuliang, Fujian, China, in USNM, examined, with the abdomen missing).

**DIAGNOSIS.**— The female epigynum of this species is similar to *L. karschi* (according to Chamberlin, 1924). Unfortunately, the holotype lacks the abdomen. Further collection of both male and female from the type locality is needed.

**DESCRIPTION.**— See Chamberlin (1924). Female chelicerae with three promarginal, two retromarginal teeth. Male unknown.

**DISTRIBUTION.**— China (Fujian) (Map 27).

**MATERIAL EXAMINED.**— CHINA: **Fujian**: Kuliang, 2400 m, female holotype (with abdomen missing) (N. Gist Gee, USNM, No. 883).

***Longicoelotes senkakuensis* (Shimojana, 2000), NEW COMBINATION**

Map 27

*Coelotes senkakuensis* Shimojana, 2000:175, figs. 44–49 (female holotype from Senkaku, deposited in NSMT, not examined).

**DIAGNOSIS.**— The female of this species appears similar to *L. karschi* on the basis of the published description but can be distinguished by the small spermathecal heads and the differences in shapes between their epigynum.

**DESCRIPTION.**— See Shimojana (2000). Female chelicerae with three promarginal, two retro-marginal teeth. Male unknown.  
**DISTRIBUTION.**— Senkaku (Map 27).  
**MATERIAL EXAMINED.**— None.

**Genus *Platocoelotes* Wang, 2002**

*Platocoelotes* Wang, 2002:119 (type species, by original designation, *Coelotes impletus* Peng and Wang, 1997 from China).

**DIAGNOSIS.**— The female can be easily recognized by the absence of epigynal teeth, the presence of an anteriorly situated epigynal cavity (depression), the deep, posteriorly situated epigynal hoods, and the long, strongly convoluted spermathecae, and the male by the presence of two patellar apophyses, the elongated cymbial furrow, the presence of a conductor posterior apophysis, the long embolus, and the absence of median apophysis (Figs. 75–78).

**PHYLOGENETIC PLACEMENT.**— The absence of both epigynal teeth and median apophysis supports the sister group relationship between *Platocoelotes* and *Spiricoelotes*, together they remain unresolved with the genera *Draconarius*, *Asiacoelotes*, and *Bifidocoelotes* (Wang, 2002).

- DESCRIPTION.**— See Wang (2002).  
**DISTRIBUTION.**— China (Map 28).  
**COMPOSITION.**— 5 species, including 1 new species:  
1. *Platocoelotes impletus* (Peng and Wang, 1997)  
2. *Platocoelotes icohamatoides* (Peng and Wang, 1997)  
3. *Platocoelotes icohamatus* (Zhu and Wang, 1991)  
4. *Platocoelotes kailiensis* Wang, sp. nov.  
5. *Platocoelotes lichuanensis* (Chen and Zhao, 1998)

**Key to the Species of the Genus *Platocoelotes***

- 1. Males (those of *P. icohamatus* and *P. icohamatoides* unknown)..... 2  
Females (those of *P. lichuanensis* unknown, and *P. icohamatus* not examined)..... 4
- 2. Embolus with base extending prolaterally (Figs. 75D; 78A) ..... 3  
Embolus with base extending posteriorly (Fig. 77D)..... *kailiensis*
- 3. Conductor with apical apophyses large, as in Fig. 78A..... *lichuanensis*  
Conductor with apical apophyses small, as in Fig. 75D ..... *impletus*
- 4. Spermathecal bases large, transversely extending; spermathecal stalks broad, with less than three loops (Fig. 75B)..... *impletus*  
Spermathecal bases small, close together, longitudinally extending, spermathecal stalks narrow, with at least three loops (Figs. 76B; 77B)..... 5
- 5. Spermathecal stalks extremely long, with at least five loops (Fig. 77B)..... *kailiensis*  
Spermathecal stalks moderately long, with 3–4 loops (Fig. 76B) ..... *icohamatoides*

***Platocoelotes impletus* (Peng and Wang, 1997)**

Figures 75A–E; Map 28  
*Coelotes impletus* Peng and Wang, 1997:328, figs. 11–19 (2 male and 2 female types from Zhangjiajie, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:375, figs. 220D–E, 222H, 223K.  
*Platocoelotes impletus*: Wang, 2002:122, figs. 336–348.

**DIAGNOSIS.**— The female of this species is similar to *P. icohamatus*, unfortunately the vulva of *P. icohamatus* was not illustrated in the original paper and the specimens of *P. icohamatus* were not available for this research. The female can be distinguished from other *Platocoelotes* by the anteriorly diverging spermathecae and less looped copulatory ducts (two loops) (Figs. 75A–B). The male can be differentiated from *P. kailiensis* by the prolaterally extending embolic base, and from *P. lichuanensis* only by the smaller conductor apical apophyses (Figs. 75C–E).

**DESCRIPTION.**— See Peng and Wang (1997) and Wang (2002). Chelicerae with three promarginal and two retromarginal teeth. Female epigynum without teeth; epigynal hoods situated posteriorly, near epigastric margin; atrium large, longitudinally elongated; epigynum with anteriorly situated cavity; copulatory ducts short; spermathecal heads small; spermathecal bases extending transversely; spermathecal stalks broad, with less than three loops (Figs. 75A–B). Male palp with two patellar apophyses; retrolateral tibial apophysis long, occupying almost entire tibial length; lateral tibial apophysis small, widely separated from RTA; cymbial furrow about half cymbial length or slightly shorter; conductor broad, with a long, posteriorly extending apophysis and an anteriorly extending finger-like apophysis; conductor dorsal apophysis broad; conductor basal lamella small; embolus posterior in origin, long; median apophysis absent (Figs. 75C–E).

**DISTRIBUTION.**— China (Hunan) (Map 28).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Zhangjiajie, August 18–20, 198?, 2 male and 2 female types (J.F. Wang and X.J. Peng, HBI).

*Platocoelotes icohamatoides* (Peng and Wang, 1997)

Figures 76A–B; Map 28

*Coelotes icohamatoides* Peng and Wang, 1997:328, figs. 5–10 (1 female paratype from Naer Mt., Fenghuang, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:375, figs. 219Q–R.

*Platocoelotes icohamatoides*: Wang, 2002:122.

**DIAGNOSIS.**— The female of this species is similar to *P. kailiensis* but can be distinguished by the less looped spermathecal stalks (with 3 loops) (Figs. 76A–B).

**DESCRIPTION.**— Described by Peng and Wang (1997). Chelicerae with three promarginal and two retromarginal teeth. Female epigynum without epigynal teeth; epigynal hoods situated posteriorly near epigastric margin; atrium large, longitudinally elongated; epigynum with anteriorly situated cave; copulatory ducts short; spermathecal heads small; spermathecal bases extending longitudinally, situated close together; spermathecal stalks broad, with at least three loops (Figs. 76A–B). Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 28).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Fenghuang, Naer Mt., 1 female paratype (J.F. Wang, HBI).

*Platocoelotes icohamatus* (Zhu and Wang, 1991)

Map 28

*Coelotes icohamatus* Zhu and Wang, 1991:2, fig. 5–7 (female holotype, male and female paratypes from Sichuan, China, in NBUMS, not examined).— Song, Zhu and Chen, 1999:375, figs. 220A, 222F, 223I.

*Platocoelotes icohamatus*: Wang, 2002:122.

**DIAGNOSIS.**— The female epigynum of this species is identical to *P. impletus*, unfortunately the vulva was not illustrated in the original paper and the specimens were not available for this research. The male paratypes are similar to *D. calcariformis* and might be mistakenly matched.



**NOTES.**— Judging from the illustrations by Zhu and Wang (1991, figures 6–7) and Song, Zhu and Chen (1999, figures 222F, 223I), the male paratypes from the same locality with female holotype may be mistakenly matched.

**DESCRIPTION.**— See Zhu and Wang (1991). Chelicerae with three promarginal and two retromarginal teeth. Female epigynum without epigynal teeth; epigynal hoods situated posteriorly near epigastric margin; atrium large, longitudinally elongated; epigynum with anteriorly situated cave.

**DISTRIBUTION.**— China (Sichuan) (Map 28).

**MATERIAL EXAMINED.**— None.

***Platocoelotes kailiensis* Wang, sp. nov.**

Figures 77A–E; Map 28

**TYPES.**— Holotype male from Kaili, Guizhou, China (X.P. Wang; October 3, 1997), 1 female paratype from Shanchahe Cave, Maolai Natural Reserve, Libo, Guizhou, China (X.P. Wang; October 6, 1997), 1 female paratype from WongAng Cave, Maolai Natural Reserve, Libo, Guizhou, China (X.P. Wang; October 9, 1997), deposited in IZB.

**DIAGNOSIS.**— The female of this new species is similar to *P. icohamatoides* but can be distinguished by the long, looped copulatory ducts (with at least 5 loops) (Figs. 77A–B). The male can be distinguished by the posterior extension of the embolic base and the strongly expanded cymbial furrow (Figs. 77C–E).

**FEMALE.**— Total length 6.47. Carapace 3.19 long, 2.15 wide. Promargin of chelicera with three teeth, retromargin with two. Eye sizes and interdistances: AME 0.10, ALE 0.17, PME 0.15, PLE 0.16; AME-AME 0.08, AME-ALE 0.06, PME-PME 0.09, PME-PLE 0.16, ALE-PLE 0.05, AME-PME 0.14. Leg measurements: I: 12.3 (3.28, 4.18, 2.91, 1.92); II: 10.4 (2.68, 3.44, 2.60, 1.72); III: 9.39 (2.51, 2.89, 2.52, 1.47); IV: 12.6 (3.22, 4.05, 3.50, 1.78). Female epigynum without teeth; epigynal hoods situated posteriorly near epigastric furrow; atrium longitudinally elongated; epigynum with anterior cavity; copulatory ducts short; spermathecal heads small; spermathecal bases small, contiguous, longitudinally extending; spermathecal stalks strongly elongated, slender, highly convoluted with at least 5 loops (Figs. 77A–B).

**MALE.**— Total length 8.47. Carapace 3.90 long, 2.67 wide. Promargin of chelicera with three teeth, retromargin with two. Eye sizes and interdistances: AME 0.18, ALE 0.19, PLE 0.19; PME 0.19, AME-AME 0.08, AME-ALE 0.05, PME-PME 0.13, PME-PLE 0.15. Leg measurements: I: 17.5 (4.60, 5.79, 4.42, 2.70); II: 15.5 (4.22, 4.90, 3.91, 2.44); III: 14.1 (3.75, 4.18, 3.93, 2.19); IV: 18.4 (4.70, 5.61, 5.61, 2.49). Palp with two patellar apophyses; RTA long, occupying almost entire tibial length; lateral tibial apophysis broad; cymbial furrow elongate, at least 2/3 cymbial length; conductor broad, with a posteriorly extending apophysis and an anteriorly extending finger-like apophysis; conductor dorsal apophysis broad; conductor basal lamella small; embolus posterior in origin; embolic base extending posteriorly; without median apophysis (Figs. 77C–E).

**DISTRIBUTION.**— China (Guizhou) (Map 28).

**OTHER MATERIAL EXAMINED.**— None.

***Platocoelotes lichuanensis* (Chen and Zhao, 1998)**

Figures 78A–B; Map 28

*Coelotes lichuanensis* Chen and Zhao, 1998:3, figs. 1(1–3) (male holotype from Lichuan, Hubei, China, in HUW, examined).

*Platocoelotes lichuanensis*: Wang, 2002:122.

**DIAGNOSIS.**— The male of this species is similar to *P. impletus* but can be recognized by the large lateral tibial apophysis and the relatively strong conductor apical apophyses (Figs. 78A–B).

**DESCRIPTION.**— Described by Chen and Zhao (1998). Male palp with two patellar apophyses; RTA long, occupying almost entire tibial length; lateral tibial apophysis broad; cymbial furrow elongate, at least half cymbial length; conductor broad, with a posteriorly extending apophysis and an anteriorly extending finger-like apophysis; conductor dorsal apophysis broad, lamella small; embolus posterior in origin; embolic base extending prolaterally; without median apophysis (Figs. 78A–B). Female unknown.

**DISTRIBUTION.**— China (Hubei) (Map 28).

**MATERIAL EXAMINED.**— CHINA: **Hubei:** Lichuan, September 21, 1977, male holotype (HUW, 77–598).

**Genus *Spiricoelotes* Wang, 2002**

*Spiricoelotes* Wang, 2002:129 (type species, by original designation, *Coelotes zonatus* Peng and Wang, 1997 from China).

**DIAGNOSIS.**— The female can be easily recognized by the absence of epigynal teeth and the long, strongly convoluted spermathecae, and the male by the strongly curved patellar apophysis, the elongated cymbial furrow, the absence of a conductor dorsal apophysis, and the slender, anteriorly extending, spiraled conductor (Figs. 79–80).

**PHYLOGENETIC PLACEMENT.**— The absence of both epigynal teeth and median apophysis supports the sister group relationship between *Platocoelotes* and *Spiricoelotes*, together they remain unresolved with the genera *Draconarius*, *Asiacoelotes*, and *Bifidocoelotes* (Wang, 2002).

**DESCRIPTION.**— See Wang (2002)

**DISTRIBUTION.**— China, Japan (Map 29).

**COMPOSITION.**— 3 species, including 1 new species:

- 1. *Spiricoelotes urumensis* (Shimojana, 1989)
- 2. *Spiricoelotes zonatus* (Peng and Wang, 1997)  
*Coelotes laoyingensis* Chen and Zhao, 1997
- 3. *Spiricoelotes pseudozonatus* Wang, sp. nov.

**Key to the Species of the Genus *Spiricoelotes***

- 1. Female ..... 2  
Male (those of *S. pseudozonatus* unknown) ..... 4
- 2. Spermathecal stalks looped surrounding copulatory ducts (Fig. 80B) ..... 3  
Spermathecal stalks not looped surrounding copulatory ducts (Fig. 79B) .... *pseudozonatus*
- 3. Spermathecal bases extending medially; spermathecal stalks situated close together (Fig. 80B) ..... *zonatus*  
Spermathecal bases extending anteriorly; spermathecal stalks widely separated. . . . *urumensis*
- 4. Conductor long, almost reaching distal end of cymbium ..... *urumensis*  
Conductor short, only reaching half way to distal end of cymbium (Figs. 80C–E) . . . . *zonatus*

***Spiricoelotes pseudozonatus* Wang, sp. nov.**

Figures 79A–B; Map 29

**TYPES.**— Female holotype from Bao-guang monastery, Chengdu, Sichuan, China (May 21, 1989; P. Beron), deposited in AMNH (Coll. Deeleman).

**ETYMOLOGY.**— The specific name refers to its similarity to *S. zonatus*.

**DIAGNOSIS.**— The female of this new species can be distinguished from *S. zonatus* by the less apparent epigynal hoods, the small, medially situated atrium, and the differences in their spermathecal loops (Figs. 79A–B).

**FEMALE.**— Total length 3.31. Carapace 1.27 long, 0.94 wide. Abdomen 2.04 long, 1.45 wide. Eye sizes and interdistances: AME 0.05, ALE 0.07, PME 0.06, PLE 0.07; AME-AME 0.02, AME-ALE 0.02, PME-PME 0.07, PME-PLE 0.07. Leg measurements: I: 3.46 (1.04, 1.25, 0.71, 0.46); II: 3.76 (1.04, 1.30, 0.88, 0.54); III: 2.88 (0.82, 0.95, 0.69, 0.42); IV: 3.83 (1.06, 1.31, 0.88, 0.58). Promargin of chelicera with three teeth, retromargin five to six. Epigynal teeth absent; atrium small, medially situated; epigynal hoods less apparent; copulatory ducts short; spermathecal heads not visible; spermathecal bases widely separated; spermathecal stalks strongly elongated, convoluted (Figs. 79A–B).

**MALE.**— Unknown.

**DISTRIBUTION.**— China (Sichuan) (Map 29).

**OTHER MATERIAL EXAMINED.**— None.

***Spiricoelotes urumensis* (Shimojana, 1989)**

Map 29

*Coelotes urumensis* Shimojana, 1989:79, figs. 24–29 (male holotype, male and female paratypes from Ryukyu Is., in NSMT, not examined).

*Spiricoelotes urumensis*: Wang, 2002:131.

**DIAGNOSIS.**— This species is similar to *S. zonatus* but can be distinguished by the widely separated, slender spermathecal tubes of female, and the longer conductor of male.

**DESCRIPTION.**— See Shimojana (1989). Cheliceral teeth unknown. Female lacking epigynal teeth; atria small, widely separated; epigynal hoods well developed, situated anterior of atria; copulatory ducts anteriorly expanded; spermathecal bases widely separated, anteriorly extending; spermathecal stalks long, slender, widely separated, looped around copulatory ducts (Figs. A–B). Male palp with patellar apophysis long, with distal end sharply curved dorsally; RTA long; lateral tibial apophysis small; cymbial furrow about half of cymbial length; conductor long, slender, anteriorly extending; conductor dorsal apophysis absent; conductor lamella small; embolus posterior in origin, long; median apophysis absent.

**DISTRIBUTION.**— Ryukyu Is. (Map 29).

**MATERIAL EXAMINED.**— None.

***Spiricoelotes zonatus* (Peng and Wang, 1997)**

Figures 80A–E; 97I; Map 29

*Coelotes zonatus* Peng and Wang, 1997:331, figs. 32–36 (2 male and 2 female paratypes, holotype not indicated, from Changsha, Hunan, China, in HBI, examined).— Song, Zhu and Chen, 1999:376, figs. 220H–I, 222I, 223L.

*Coelotes laoyingensis* Chen and Zhao, 1997:89, figs. 5–6 (female holotype and 1 female paratype from

Laoying, Wudangshan, Hubei, China, in HUW, examined).— Song, Zhu and Chen, 1999:388, figs. 226O, P, 227P, 229B.

*Spiricoelotes zonatus*: Wang, 2002:131.

**DIAGNOSIS.**— This species is similar to *S. urumensis* but can be distinguished by the broad spermathecal tubes of female (Figs. A–B), and the relatively short conductor of male (Figs. C–E).

**DESCRIPTION.**— Described by Peng and Wang (1997) and Wang (2002). Chelicerae with five promarginal and five retromarginal teeth. Female epigynum without epigynal teeth; atria small, widely separated; epigynal hoods well developed; copulatory ducts short; spermathecal heads small; spermathecal bases situated close together, medially extending; spermathecal stalks long, slender, situated close together, looped around copulatory ducts (Figs. A–B). Male palp with patellar apophysis long, with distal end sharply curved dorsally; RTA long; lateral tibial apophysis small; cymbial furrow longer than half of cymbial length; conductor long, slender, anteriorly extending; conductor dorsal apophysis absent; conductor lamella small; embolus posterior in origin, long; median apophysis absent (Figs. C–E).

**DISTRIBUTION.**— China (Hubei, Hunan, Jiangsu, Sichuan) (Map 29).

**MATERIAL EXAMINED.**— CHINA: **Hunan**: Changsha, January 7, 1985, 2 male and 2 female paratypes (J.F. Wang, HBI); Changsha, Yuelushan, June 1995, 1 female (X.P. Wang, IZB). **Sichuan**: Chengdu, Bao-guang Monastery, May 21, 1989, 2 males (P. Beron, Coll. Delleman). **Jiangsu**: Nanjing, Zijin (Purple) Mt., 350–450 m, October 9, 1988, 1 female (P. Beron, Coll. Delleman). **Hubei**: Wudangshan, Laoying, May 10, 1982, female holotype and 1 female paratype of *Coelotes laoyingensis* (HUW).

### Genus *Tegecoelotes* Ovtchinnikov, 1999

*Tegecoelotes* Ovtchinnikov, 1999:68 (type species, by original designation, *Coelotes bicaudatus* Paik, 1976, from Korea).— Wang, 2002:133.

**DIAGNOSIS.**— The female can be distinguished by the broad epigynal teeth, the reduced atrium, and the short copulatory ducts. The male can be recognized by the elongated patella (except in *T. muscicapus* and *T. michikoe*) and the not spoon-like median apophysis (Figs. 81–84). Chelicerae with three promarginal and three retromarginal teeth.

**PHYLOGENETIC PLACEMENT.**— Remains unresolved with *Leptocoelotes* and the clade with spoon-like median apophysis and slender epigynal teeth (Wang 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— China, Japan, Korea, Far eastern Russia (Map 30).

**COMPOSITION.**— 5 species:

1. *Tegecoelotes corasides* (Bösenberg and Strand, 1906)  
*Coelotes corasoides* Platnick, 1989
2. *Tegecoelotes secundus* (Paik, 1971)  
*Tegecoelotes bicaudatus* (Paik, 1976)  
*Coelotes erraticus* Nishikawa, 1983
3. *Tegecoelotes ignotus* (Bösenberg and Strand, 1906)  
*Agelena ignota* Bösenberg and Strand, 1906
4. *Tegecoelotes michikoe* (Nishikawa, 1977)
5. *Tegecoelotes muscicapus* (Bösenberg and Strand, 1906)

Key to the Species of the Genus *Tegecoelotes*

1. Male (those of *ignotus* unknown) ..... 2  
     Female (those of *muscicapus* unknown) ..... 4
2. Patella long, with one patellar apophysis (Figs. 81D-F) ..... 3  
     Patella short, with two patellar apophyses (Figs. 84A-C) ..... *muscicapus*, *michikoeae*
3. Conductor apex broad, slightly curved anteriorly (Figs. 82C-F) ..... *corasides*  
     Conductor apex slender, slightly curved posteriorly (Figs. 81C-F) ..... *secundus*
4. Epigynal teeth close together, separated by less than their width (Fig. 82A) ..... 5  
     Epigynal teeth separated by approximatedly twice their width ..... *michikoeae*
5. Spermathecal bases without apophyses ..... 6  
     Spermathecal bases with long, anteriorly extending apophyses (Fig. 83B) ..... *ignotus*
6. Spermathecal heads slender (Fig. 82B) ..... *corasides*  
     Spermathecal heads broad (Fig. 81B) ..... *secundus*

*Tegecoelotes secundus* (Paik, 1971)

Figures 81A-F; Map 30

*Tegenaria secunda* Paik, 1971:22, figs. 8–14 (male holotype from Korea, deposited in Kyungpook National University, Taegu, Korea, not examined).— Paik, 1978:360, figs. 162.1–2.

*Coelotes bicaudatus* Paik, 1976:81, figs. 3, 13–15 (female holotype from Mt. Ode, Korea, deposited in Kyungpook National University, Taegu, Korea, not examined).— Paik, 1978:334, figs. 147.1–2.

*Coelotes erraticus* Nishikawa, 1983:125, figs. 1–6 (male and female types from Mt. KomA-gA-take, Tazawako-cho, Senboku-gun, Akita, Japan, in NSMT, not examined).—Yaginuma, 1971:93, fig. 82.1–2;— Matsuda, 1986:88, figs. 13–16;—Yaginuma, 1986:151, fig. 80.3;— Wang and Zhu, 1991:5, figs. 13–16;— Song, Zhu and Chen, 1999:375, figs. 217M–N, 219G, N. (First synonymized by Ovtchinnikov, 1999.)

*Tegecoelotes bicaudatus* Ovtchinnikov, 1999:68, figs. 16–20 (male first described).— Wang, 2002:134, figs. 375–383. (First Synonymized by Marusik and Koponen, 2000.)

*Tegecoelotes secunda*: Marusik and Koponen, 2000:56.

**DIAGNOSIS.**— This species is similar to *T. corasides* but can be distinguished by the relatively narrow epigynal teeth, the small copulatory ducts, the differences in shapes between the spermathecal tubes of female (Figs. 81A–B) and the slender, posteriorly curved conductor apex, and the strongly spiraled median apophysis of male (Figs. 81C–F).

**DESCRIPTION.**— Described by Paik (1976). Chelicerae with three promarginal and three retro-marginal teeth. Female epigynal teeth broad, close together; atrium small; copulatory ducts short; spermathecal heads large; spermathecae with bases small, stalks broad, short, laterally extending (Figs. 81A–B). Male palp with patella strongly elongated; patellar apophysis present; RTA long; lateral tibial apophysis large; cymbial furrow short; conductor long, with slender, slightly curved apex; conductor dorsal apophysis present; conductor lamella small; embolus short, prolateral in origin; median apophysis not spoon-like, long, with sharp, strongly spiraled apex and membranous base (Figs. 81C–F).

**DISTRIBUTION.**— China (Jilin), Korea, Japan, Russia (Far East) (Map 30).

**MATERIAL EXAMINED.**— RUSSIA: Far East, S-Primorie, “Kedrovaya Pad” Reservation in a living house, June 12 – December 24, 1977, 2 males and 2 females (B.P. Zakharov, SZM). KOREA: Moon-Kyang-Sae-Jae, 1 male, August 20, 1990 (J.P. Kim, KAI).

***Tegecoelotes corasides* (Bösenberg and Strand, 1906)**

Figures 82A–F; Map 30

*Tegenaria corasides* Bösenberg and Strand, 1906:301, fig. 459 (fig. 460 is *Paracoelotes luctuosus*) (male and female types, holotype not indicated, from Saga, Japan, in SMF, examined).—Yaginuma, 1957:17, fig. 2; —Yaginuma, 1960:92, fig. 81.8;—Yaginuma, 1971:92, fig. 81.8.

*Coras luctuosus*: Saito, 1934:342, figs. 27, 53.—Saito, 1959:43, fig. 16A–C (misidentification).

*Coelotes modestus*: Nishikawa, 1974:177, figs. 17–19.—Nishikawa, 1977: figs. 19–20 (misidentification).

*Coelotes corasides*: Yaginuma, 1986:148, fig. 80.1.—Chikuni, 1989:103, fig. 21.

*Coelotes corasoides*: Platnick, 1989:422 (lapsus).

*Tegecoelotes corasides*: Wang, 2002:134.

**DIAGNOSIS.**— This species is similar to *T. secundus* but can be distinguished by the relatively broad epigynal teeth, the large copulatory ducts, the differences in shapes between the spermathecal tubes of female (Figs. 82A–B) and the broad, anteriorly curved conductor apex, and the simple median apophysis of male (Figs. 82C–F).

**DESCRIPTION.**— Described by Bösenberg and Strand (1906). Chelicerae with three promarginal and three retromarginal teeth. Epigynal teeth broad, close together; atrium small; copulatory ducts large; spermathecal heads small; spermathecae with bases small, stalks broad, short (Figs. 82A–B). Male palp with patella strongly elongated; patellar apophysis present; RTA long; lateral tibial apophysis large; cymbial furrow short; conductor long, with broad, anteriorly curved apex; conductor dorsal apophysis present; conductor lamella small; embolus short, prolateral in origin; median apophysis not spoon-like, long (Figs. 82C–F).

**DISTRIBUTION.**— Japan (Map 30).

**MATERIAL EXAMINED.**— JAPAN: Saga, 1 male and 1 female types (W. Donitz, SMF, 4808); Saga, 2 male and 9 female paratypes (W. Donitz, SMF, 4809); Cross Kamdeals, 1 male and 1 female (Donitz, ZMB, 31192); Kauagawa, February 18, 1905, 1 male (H. Sauter, ZMB, 31191); Camp Fuji, March 3, 1955, 1 male (V. Cambl, CAS).

***Tegecoelotes ignotus* (Bösenberg and Strand, 1906)**

Figure 83A–B; Map 30

*Agelena ignota* Bösenberg and Strand, 1906:299, fig. 466 (2 female types, holotype not indicated, from Japan, in SMF, examined).—Ishinoda, 1957:12, fig. 3.

*Coelotes ignotus*: Lehtinen, 1967:224;—Nishikawa, 1974:178, fig. 33.

*Tegecoelotes ignotus*: Wang, 2002:134.

**DIAGNOSIS.**— The female of this species can be easily recognized by the broad, anteriorly situated epigynal teeth, the broad copulatory ducts, and the long, slender spermathecal diverticula (Figs. 83A–B).

**DESCRIPTION.**— Described by Bösenberg and Strand (1906). Chelicerae with three promarginal and three retromarginal teeth. Female epigynum with epigynal teeth broad, more or less rounded, situated anteriorly; atrium small; copulatory ducts broad, extending laterally; spermathecal heads not visible; spermathecal bases with long, anteriorly extending diverticula; spermathecal stalks slender, anteriorly extending (Figs. 83A–B). Male unknown.

**DISTRIBUTION.**— Japan (Map 30).

**MATERIAL EXAMINED.**— JAPAN: no detailed label, 2 female types (W. Donitz, SMF, 4697).

***Tegecoelotes michikoe* (Nishikawa, 1977)**

Map 30

*Coelotes michikoe* Nishikawa, 1977:39, figs. 13–18 (female holotype, male and female paratypes from Minoo, Osaka Prefecture, Japan, deposited in the Osaka Museum of Natural History, Osaka, and in the Arachnological Society of Japan, Ohtemon-Gakuin University, Osaka, Japan, not examined).— Chikuni, 1977:56, fig. 1.3;— Yaginuma, 1986:151, fig. 80.2;— Chikuni, 1989:102, fig. 20.

*Tegecoelotes michikoe*: Wang, 2002:134.

**DIAGNOSIS.**— The male of this species is similar to *T. muscicapus* and can only be distinguished by the less expanded conductor apex. The widely separated epigynal teeth can distinguish females from other *Tegecoelotes* (except *T. muscicapus*, which is not known).

**DESCRIPTION.**— See Nishikawa (1977). Chelicerae with three promarginal and three retromarginal teeth. Female epigynal teeth broad, widely separated by at least twice their width; atrium small; spermathecal bases extending medially; spermathecal stalks situated close together. Male palp with patella short, approximately tibial length; patella with two apophyses, with dorsal one small; RTA long; lateral tibial apophysis present; cymbial furrow short; conductor long, with anteriorly curved apex; conductor dorsal apophysis present; conductor lamella small; embolus short, prolateral in origin; median apophysis not spoon-like, with slender apex.

**DISTRIBUTION.**— Japan (Map 30).

**MATERIAL EXAMINED.**— None.

***Tegecoelotes muscicapus* (Bösenberg and Strand, 1906)**

Figure 84A–C; Map 30

*Tegenaria muscicap* Bösenberg and Strand, 1906:302, fig. 479 (male holotype from Saga, Japan, in SMF, examined).

*Tegecoelotes muscicap*: Wang, 2002:134.

**DIAGNOSIS.**— The male of this species is similar to *T. michikoe* and can only be distinguished by the relatively broad conductor apex (Figs. 84A–B).

**DESCRIPTION.**— Described by Bösenberg and Strand (1906). Chelicerae with three promarginal and three retromarginal teeth. Male palp with patella short, approximately tibial length; patella with two apophyses, with dorsal one small; RTA long; lateral tibial apophysis present; cymbial furrow short; conductor long, with broad, anteriorly curved apex; conductor dorsal apophysis present; conductor lamella small; embolus short, prolateral in origin; median apophysis not spoon-like, with slender apex (Figs. 84A–C). Female unknown.

**DISTRIBUTION.**— Japan (Map 30).

**MATERIAL EXAMINED.**— JAPAN: Saga, male holotype (W. Donitz, SMF, 4820); Saga, 1 male (W. Donitz, SMF, in the same vial as *Coelotes corasides* paratypes, 4809).

**Genus *Tonsilla* Wang and Yin, 1992**

*Tonsilla* Wang and Yin, 1992:263 (type species, by original designation, *Tonsilla truculenta* Wang and Yin, 1992 from China).— Platnick, 1997:671;— Wang, 2002:136.

**DIAGNOSIS.**— The female can be easily recognized by the large epigynal atrium, the posterior extension of anterior atrial margin, the median, closely situated epigynal teeth, and the large copulatory ducts, and the male by the long patellar apophysis, the short cymbial furrow, and the bifur-

cate (or lobed) conductor (Figs. 85–95). Cheliceral promargin with three teeth, retromargin with two.

**PHYLOGENETIC PLACEMENT.**— The presence of a large atrium and the posteriorly extending anterior atrial margin support the sister group relationship between *Tonsilla* and *Paracoelotes*. Together they are the sister group of the clade with two retromarginal cheliceral teeth and large conductor lamella (Wang 2002).

**DESCRIPTION.**— See Wang (2002).

**DISTRIBUTION.**— Central China (Maps 31–32)

**COMPOSITION.**— 7 species, including 1 new species and 2 new combinations:

**The *truculenta* group species**

- 1. *Tonsilla eburniformis* Wang and Yin, 1992
- 2. *Tonsilla imitata* Wang and Yin, 1992
- 3. *Tonsilla truculenta* Wang and Yin, 1992

**The *variegatus* group species**

- 4. *Tonsilla lyratus* (Wang et al., 1990), NEW COMBINATION
- 5. *Tonsilla tautispinus* (Wang et al., 1990), NEW COMBINATION
- 6. *Tonsilla variegatus* (Wang et al., 1990)
- 7. *Tonsilla makros* Wang, sp. nov.

**Key to Species of the Genus *Tonsilla***

- 1. Male ..... 2  
Female ..... 4
- 2. Conductor bifurcate (Figs. 94C-E) ..... 3  
Conductor positeriorly lobed (Figs. 86C-E) ..... *truculenta*
- 3. Conductor strongly bifurcate, with anterior apophysis slightly curved anteriorly (Figs. 94D, E) ..... *variegatus*  
Conductor slightly bifurcate, apex not curved (Figs. 95A–C) ..... *makros*
- 4. Epigynal teeth short, separated by at least their width, spermathecae broad, not elongated ..... 5  
Epigynal teeth long, slender, close together or separated by less than their width, spermathecae longitudinally elongate (Figs. 86A; 91A) ..... *truculenta, eburniformis, imitata*
- 5. Epigynal teeth situated on anterior atrial margin (Fig. 94A) ..... 6  
Epigynal teeth situated anterad of atrium, separated from anterior atrial margin (Fig. 93A) ..... *tautispinus*
- 6. Copulatory ducts strong expanded anteriorly; spermathecal heads situated anteriorly (Fig. 94B) ..... *variegatus*  
Copulatory ducts not anteriorly expanded; spermathecal heads situated laterally (Fig. 92B) ..... *lyratus*

**The “*truculenta*” Group**

The male of this group generally has the long, dorsally curved patellar apophysis and posteriorly lobed conductor; the female has the slender, closely situated epigynal teeth, and anteriorly elongated spermathecae.



***Tonsilla eburniformis* Wang and Yin, 1992**

Figures 85A–B; Map 31

*Tonsilla eburniformis* Wang and Yin, 1992:265, figs. 13–14 (female holotype from Muyu, Shenlongjia, Hubei, China, in HTU, examined).

**DIAGNOSIS.**— The female of this species is similar to *T. truculenta* and can be distinguished by the slightly separated bases of epigynal teeth, the broad septum, and the short, broad spermathecae (Figs. 85A–B).

**DESCRIPTION.**— Described by Wang and Yin (1992). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth slender, situated close together, with bases slightly separated; atrium large; septum broad; copulatory ducts situated mesad of spermathecae, slightly extending anteriorly; spermathecal heads long, extending mesad of spermathecae; spermathecae broad, widely separated (Figs. 85A–B). Male unknown.

**DISTRIBUTION.**— China (Hubei) (Map 31).

**MATERIAL EXAMINED.**— CHINA: **Hubei:** Shenlongjia, Muyu, November 12, 1992, female holotype (J.F. Wang, HTU).

***Tonsilla imitata* Wang and Yin, 1992**

Map 31

*Tonsilla imitata* Wang and Yin, 1992:264, figs. 11–12 (female holotype from Qiayang, Hunan, China, in HBI, not examined).— Song, Zhu and Chen, 1999:395, figs. 230G–H.

**DIAGNOSIS.**— The female of this species is similar to *T. truculenta* (specimen from Mitai, Guizhou, variation 5) and can only be distinguished by the slightly different epigynal teeth.

**DESCRIPTION.**— See Wang and Yin (1992). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth slender, situated close together; atrium large; copulatory ducts situated mesad of spermathecae, slightly extending anteriorly; spermathecal heads long, originating mesad of spermathecae, situated anteriorly; spermathecae broad, widely separated. Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 31).

**MATERIAL EXAMINED.**— None.

***Tonsilla truculenta* Wang and Yin, 1992**

Figures 86A–E; Map 31

*Tonsilla truculenta* Wang and Yin, 1992:263, figs. 1–10 (female holotype, 2 male and 7 female paratypes from Tianzishan, Sangzhi, Hunan, China, in HTU, examined).— Song, Zhu and Chen, 1999:395, figs. 131, 230I–L;— Wang, 2002:137, figs. 384–399.

**DIAGNOSIS.**— The female can be recognized by the slender, closely situated epigynal teeth, the broad atrium, the broad copulatory ducts, and the long spermathecae heads (Figs. 86A–B). The male can be distinguished by the long, strongly curved patellar apophysis and the presence of a lobed conductor (Figs. 86C–E).

**DESCRIPTION.**— Described by Wang and Yin (1992). Cheliceral promargin with three teeth, retromargin with two. Female epigynal teeth slender, situated close together, more or less overlapped; septum broad; copulatory ducts broad, situated mesad of spermathecae, not anteriorly extending; spermathecal heads long; spermathecae longitudinally extending, widely separated

(Figs. 86A–B). Male palp with patellar apophysis long, dorsally curved; RTA long; lateral tibial apophysis present, widely separated from RTA; cymbial furrow short; conductor lobed; conductor dorsal apophysis slender, with apex slightly toothed; conductor lamella small; median apophysis spoon-like, elongated (Figs. 86C–E).

**DISTRIBUTION.**— China (Guizhou, Hunan, Sichuan) (Map 31).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Sangzhi, Tianzishan, October 27, 1989, female holotype, male allotype, 1 male and 7 female paratypes (J.F. Wang, HTU).

**VARIATIONS.**— Further collection and examination of this species shows strong variation in both male and female genitalia, which includes the size and shape of patellar apophysis, the shape of conductor, and the shape of conductor dorsal apophysis of male; and the shape and position of epigynal teeth, the size and shape of septum, the atrial shape, the size and shape of spermathecae, and the shape of copulatory ducts of female. It is likely that the species *T. eburniformis* and *T. imitata* also fall into those variations. Further collections of male specimens from above two species localities are needed.

**VARIATION 1.** CHINA: **Hunan:** Sangzhi, Tianzishan, October 27, 1989, 6 male and 2 female paratypes of *T. truculenta* (J.F. Wang, HTU). From the same locality with female holotype and male allotype, but differs by the elongated patellar apophysis, the small conductor lobe, the sharp, none toothed apex of conductor dorsal apophysis of male (Figs. 87C–D) and by the slender septum and the anteriorly extending, bifurcate copulatory ducts of female (Figs. 87A–B).

**VARIATION 2.** CHINA: **Hunan:** Sangzhi, Tianzishan, October 27, 1989, 1 female paratype of *T. truculenta* (J.F. Wang, HTU). From the same locality with female holotype and male allotype, but differs by the different atrial shape, the anteriorly extending, broad copulatory ducts, and the short, broad spermathecae of female (Figs. 88A–B).

**VARIATION 3.** CHINA: **Sichuan:** Chunqing, Jiyunshan, October 26, 1997, 2 females and 1 male (X.P. Wang, HTU). Differs by the short patellar apophysis, the broad conductor lobe, and the slightly bifurcate conductor dorsal apophysis of male (Figs. 89C–E) and the relatively strong epigynal teeth, the slightly anterior extension of copulatory ducts, the short, broad spermathecae of female (Figs. 89A–B).

**VARIATION 4.** CHINA: **Guizhou:** Guiyang, campus of Guizhou Teachers University, October 30, 1997, 1 male (X.P. Wang, HTU). Differs by the blunt conductor apex, the large conductor lobe, and the short, sharply pointed patellar apophysis of male (Figs. 90A–B).

**VARIATION 5.** CHINA: **Guizhou:** Meitan, August 1981, 1 female paratype of *T. truculenta* (F.J. Li, HTU). **Hunan:** Chengbu, August 21, 1982, 1 female paratype of *T. truculenta* (J.F. Wang, HTU). Differs by the unique copulatory ducts, the short, broad spermathecae (Fig. 91A–B, female paratype from Meitan, Guizhou).

### The “*variegatus*” Group

The male of this group typically has the strongly elongated patellar apophysis (as long as patellar length) and non-lobed, more or less bifurcate conductor; the female has the short, slightly separated epigynal teeth and short spermathecae.

### *Tonsilla lyratus* (Wang et al., 1990), NEW COMBINATION

Figures 92A–B; 97H; Map 32

*Coelotes lyratus* Wang et al., 1990:200, figs. 55–56 (female holotype from Tianpingshan, Sangzhi, Hunan China, in HBI, examined).— Song, Zhu and Chen, 1999:376, figs. 220T–U.

**DIAGNOSIS.**— The female of this species is similar to *T. tautispinus* but can be distinguished

by the closely situated epigynal teeth and atrium, the anteriorly situated spermathecal heads, and the anterior extension of spermathecae (Fig. 92A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retro-marginal with two. Female epigynal teeth situated close together, slightly separated from anterior atrial margin; atrium large; epigynal hoods posteriorly situated, near epigastric furrow; copulatory ducts broad, situated mesad of spermathecae; spermathecal heads anteriorly situated; spermathecae broad, anteriorly extending, slightly zig-zaged (Figs. 92A–B). Male unknown.

**DISTRIBUTION.**— China (Hunan) (Map 32).

**MATERIAL EXAMINED.**— CHINA: **Hunan:** Sangzhi, Tianpingshan, October 16, 1986, female holotype (J.F. Wang, HBI).

***Tonsilla tautispinus* (Wang et al., 1990), NEW COMBINATION**

Figures 93A–B; Map 32

*Coelotes tautispinus* Wang et al., 1990:190, figs. 32–33 (female holotype from Lushan, Jiangxi, China, in HBI, examined).— Song, Zhu and Chen, 1999:378, figs. 225K–L.

**DIAGNOSIS.**— The female of this species is similar to *T. lyratus* but can be distinguished by the widely separated epigynal teeth and atrium, the laterally situated spermathecal heads, and the lateral extension of spermathecae (Fig. 93A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retro-marginal with two. Female epigynal teeth close together, anteriorly situated, wide apart from atrium; atrium large; epigynal hoods medially situated; copulatory ducts broad, situated anterad of spermathecae; spermathecal heads laterally originating and extending; spermathecae broad, short, slightly extending laterally (Figs. 93A–B). Male unknown.

**DISTRIBUTION.**— China (Jiangxi) (Map 32).

**MATERIAL EXAMINED.**— CHINA: **Jiangxi:** Lushan, June 15, 1987, female holotype (J.F. Wang, HBI).

***Tonsilla variegatus* (Wang et al., 1990)**

Figures 94A–F; Map 32

*Coelotes variegatus* Wang et al., 1990:184, figs. 20–24 (female holotype and 1 male paratype from Huangshan, Anhui, China, in HBI, examined).— Song, Zhu and Chen, 1999:388, figs. 226E–F, 227N, 228O.

*Tonsilla variegatus*: Wang, 2002:136.

**DIAGNOSIS.**— The male of this species is similar to *T. makros* but can be distinguished by the slightly spiraled, strongly bifurcate conductor and the relatively long median apophysis (Figs. 94C–F). The female can be recognized by the broad atrium, the large copulatory ducts, the posteriorly originated spermathecal heads, and the small spermathecae (Figs. 94A–B).

**DESCRIPTION.**— Described by Wang et al. (1990). Cheliceral promargin with three teeth, retro-marginal with two. Female epigynal teeth short, close together, situated anteriorly close to anterior atrial margin; atrium large; copulatory ducts broad, strongly expanded anteriorly; spermathecal heads long, originating posteriorly and extending laterally; spermathecae small (Figs. 94A–B). Male palp with patellar apophysis strongly elongated, at least the patellar length; RTA long; lateral tibial apophysis large; cymbial furrow short; conductor strongly bifurcate, with slightly spiraled apex; conductor dorsal apophysis slender, lamella small; embolus prolateral in origin; median apophysis spoon-like, transversely elongated (Figs. 94C–F).

**DISTRIBUTION.**— China (Anhui) (Map 32).

**MATERIAL EXAMINED.**— CHINA: **Anhui:** Huangshan, October 27, 1974, female holotype and male paratype (J.F. Wang and C.M. Yin, HBI).

***Tonsilla makros* Wang, sp. nov.**

Figures 95A–C; Map 32

**TYPES.**— Male holotype and male paratype from Wong-Ang, Libo Co., Guizhou, China (October 9, 1997; X.P. Wang and J.C. Ran), deposited in AMNH (holotype), IZB (1 male paratype).

**ETYMOLOGY.**— The specific name refers to the long patellar apophysis.

**DIAGNOSIS.**— The male of this species is similar to *T. variegatus* but can be distinguished by the slightly bifurcate conductor, and the relatively short median apophysis (Figs. 95A–C).

**MALES.**— Total length 6.20. Carapace 2.40 long, 2.80 wide. Cheliceral promargin with three teeth, retromargin with two. Eye sizes and interdistances: AME 0.08, ALE 0.15, PME 0.14, PLE 0.15, AME-AME 0.05, AME-ALE 0.02, PME-PME 0.04, PME-PLE 0.06, ALE-PLE 0.02, AME-PME 0.08. Leg measurements: I: 7.20 (1.84, 2.48, 1.80, 1.08); II: 6.20 (1.80, 2.08, 1.52, 0.80); III: 5.60 (1.68, 1.72, 1.48, 0.72); IV: 8.00 (2.08, 2.48, 2.44, 1.00). Male palp with patellar apophysis strongly elongated; RTA long; lateral tibial apophysis large, widely separated from RTA; cymbial furrow short; conductor slightly bifurcate; conductor dorsal apophysis slender; conductor lamella small; embolus prolateral in origin; median apophysis spoon-like, short (Figs. 95A–C).

**FEMALE.**— Unknown.

**DISTRIBUTION.**— China (Guizhou) (Map 32).

**OTHER MATERIAL EXAMINED.**— None.

## COELOTINAE DISTRIBUTION PATTERNS

Species of the spider subfamily Coelotinae are collected from North America (west to the Rocky Mountains), Europe, Central Asia, the Himalayas, and East Asia (south to Nepal and northern Vietnam). The single species recorded from Lebanon (*Coelotes coedatus* de Blauwe, 1973) could be a mistake because no further report of coelotines from this area so far. Coelotines are highly endemic species. No genus is shared between North America and Eurasia. Two genera (*Coelotes* and *Paracoelotes*) are found across Eurasia, but no species is shared between Europe and East Asia. Most species are endemic to small-restricted ranges, especially those from the Himalayas and East Asia, and only few are quite widespread and have large, but limited ranges (not beyond the boundary of Europe, Central Asia, the Himalayas, or East Asia), judging from the examined collections and available publications. East Asia is not only the richest in genera by having at least 15 (with 12 unique genera), it's also the richest in species (Table 1). Of the twenty coelotinae genera, only three of them are widely distributed across Eurasian continent (Table 2). Central Asia holds species from all three widespread genera, but lacks its own unique genus.

The genera *Coras* and *Wadotes*, with 15 and 11 species separately, are endemic to North America. They are collected from southeast Canada (southern Ontario, Southern Quebec, New Brunswick, Nova Scotia, and Newfoundland) and eastern US (west to Minnesota, Iowa, Kansas, Oklahoma, and Texas; south to northern Florida). The occurrence of one male *Coras lamellosus* (Keyserling, 1887) from Medicine Hat, Alberta suggests that *C. lamellosus* might extend its distribution west to southern Manitoba, southern Saskatchewan, and possibly North Dakota too, but this collection need to be verified.

The genera *Eurocoelotes* and *Urocoras*, with 11 and five species separately, are recorded from

TABLE 1. Numbers of Coelotinae genera and species distributed in North America, Europe, Central Asia, the Himalayas, and East Asia<sup>2</sup>

	North America	Europe	Central Asia	The Himalayas	East Asia
# of genera	2	4	3	2	15
Unique genera	2	2	0	1	12
# of species <sup>3</sup>	26	48	19	14 (>30 undescribed)	>200 (including some undescribed)

<sup>2</sup> All data from Platnick (2000–2002) and Wang (2002)

<sup>3</sup> The published data, maybe slightly different

TABLE 2. Three widespread Coelotinae genera<sup>4</sup>

	North America	Europe	Central Asia	The Himalayas	East Asia
<i>Coelotes</i>	—	yes	yes	—	yes
<i>Draconarius</i>	—	—	yes	yes	yes
<i>Paracoelotes</i>	—	yes	yes	—	yes

<sup>4</sup> All data from Platnick (2000–2002) and Wang (2002)

Europe. Most species are known from eastern and southeastern Europe (Italy, Greece, Hungary, Bulgaria, former Yugoslavia, and Turkey), and only *E. inermis* (L. Koch, 1855) is widespread from France, Germany, Poland, Switzerland, Italy, Austria, former Yugoslavia, to Bulgaria. Turkey has the richest *Urocoras* species diversity (currently two species, *U. nicomedis* (Brignoli, 1978) and *U. phthisicus* (Brignoli, 1978), and four more from author’s unpublished data).

Sister to *Urocoras* is the *Himalcoelotes*, which is exclusively limited to the region of the Himalayas. All 10 species are recorded from Nepal, including at least 2 species that extended their distribution to the Tibet side of the Himalayas.

Two genera, *Coelotes* and *Paracoelotes*, are widely distributed across Eurasia. *Coelotes*, here refers to only those species that belong to the type species clade (*C. atropos* Walckenaer, 1830), includes groups (*atropos*, *charitonovi*, *exitialis*, and *pseudoterrestris*) defined by Wang (2000). The *atropos* group species are found from Europe, Central Asia to Xinjiang, western China, and the *charitonovi* group species are only limited to Central Asia. The *pseudoterrestric* group species from Yunnan, China and the *exitialis* group species from Japan have quite allopatric distribution patterns compared with *atropos* and *charitonovi* groups. *Paracoelotes*, with 17 species, is found in Europe, Central Asia, and East Asia. Two *Paracoelotes* species are widespread in East Asia. According to the specimens examined in this study, *P. spinivulvus* is one of the common species in northern China (Jilin, Beijing, Hebei, Shanxi, Shaanxi, Gansu, and Hubei), Japan (no locality label), Korea, and Far East Russia, and another common species, *P. luctuosus*, is distributed in southern China (Hubei, Guizhou, Zhejiang, Jiangsu, Anhui, and Sichuan) and Japan (Osaka, Kobe, Yokohama, Tokyo, and Saga). The species *P. spinivulvus* and *P. luctuosus* are very similar in genitalic morphology and they distributional regions overlap in central China. Both of them were collected from Hubei (Xiangfan) and Guizhou (Guiyang) by the author.

Sister to *Paracoelotes* is the *Tonsilla*, which has seven species and is widespread in central and eastern China.

Both *Ambanus* and *Tegecoelotes* have limited distributions in northeast regions of East Asia. *Ambanus*, with 18 species, occurs in Korea, Far East Russia, and northeast China, while

*Tegecoelotes*, with five species, is mostly found in Japan. Only one *Tegecoelotes* species is found widespread in Japan, northeast China, Korea, and Far East Russia.

Sister to *Ambanus* is *Robusticoelotes*, which has only one species, from eastern China (Zhejiang and Jiangsu).

The genus *Femoracoelotes*, with two species and uniquely identified by the presence of a femoral apophysis, is found only in Taiwan Island. Together with the sister genus *Coronilla* (with five species) from central and eastern China and northern Vietnam they form the sister group of all other coelotine clades.

*Asiacoelotes*, with 15 species, occurs throughout East Asia (Japan, Korea, and China, west to Hunan and Guangdong provinces).

*Spiricoelotes*, with only three species, occurs from central and eastern China to Ryukyu Island and is sister to *Platocoelotes*, which has five central Chinese species.

*Draconarius*, with 86 species, is the most specious genus and is widespread from the Himalayas to central and eastern China. The type species, *D. venustus* from Tadzhikistan, is the only *Draconarius* species from that region. The closest published distribution sites to *D. venustus* are Nepal, Tibet and Gansu (China). Judging from this distribution pattern and the large number of undescribed species from the Himalayas (by examining Dr. J. Martens collections from his Himalaya Expeditions), *Draconarius* occurrence along the Karakoram mountain range and more *Draconarius* species in Tadzhikistan region are possible.

The remaining three genera are only recorded from China. *Bifidocoelotes*, with two species, from Hong Kong and Taiwan, *Leptocoelotes*, with two species, from Zhejiang and Taiwan, and *Longicoelotes*, with only three species, is recorded from eastern China (Zhejiang, Jiangsu, and Fujii) and Senkaku.

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**ILLUSTRATIONS  
AND  
DISTRIBUTION MAPS**

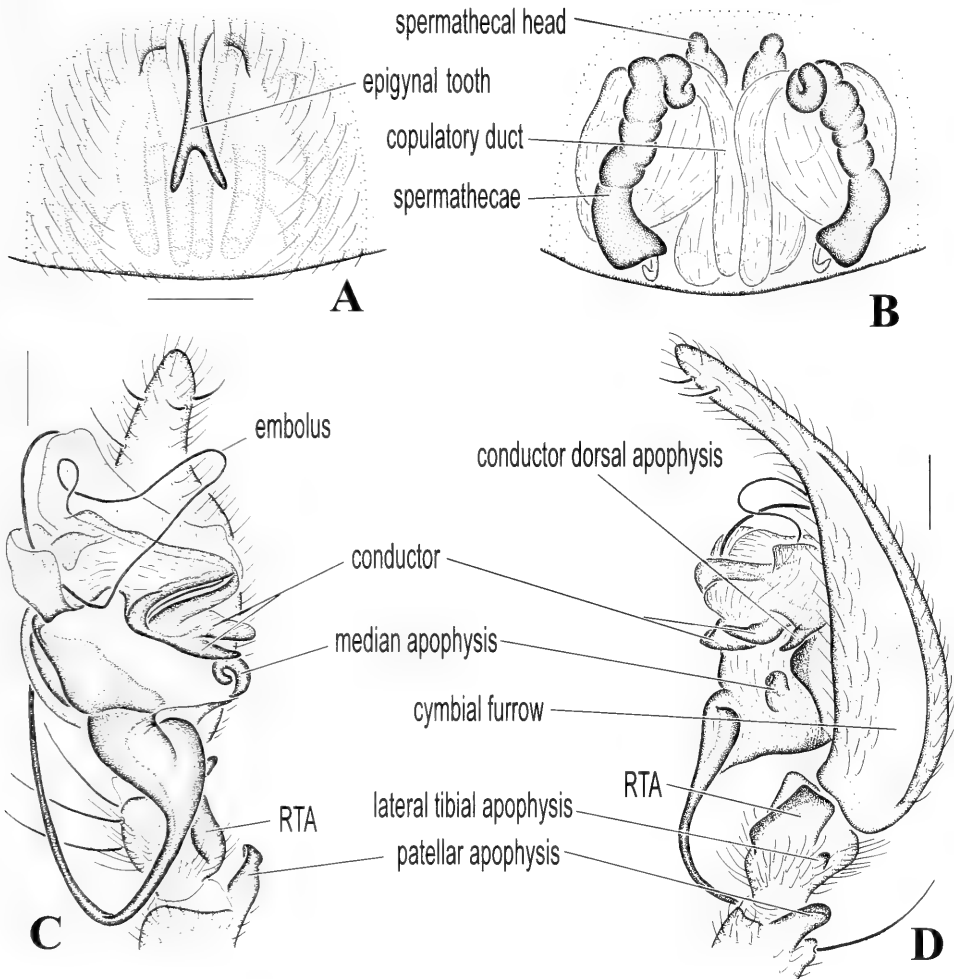


FIGURE 1. *Bifidocoelotes bifidus* (Wang, Tso and Wu). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, retrolateral view.

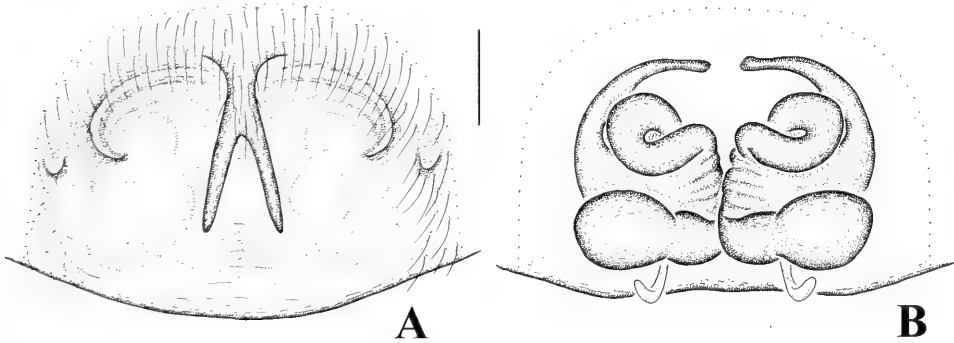


FIGURE 2. *Bifidocoelotes primus* (Fox), female. A. Epigynum. B. Vulva.

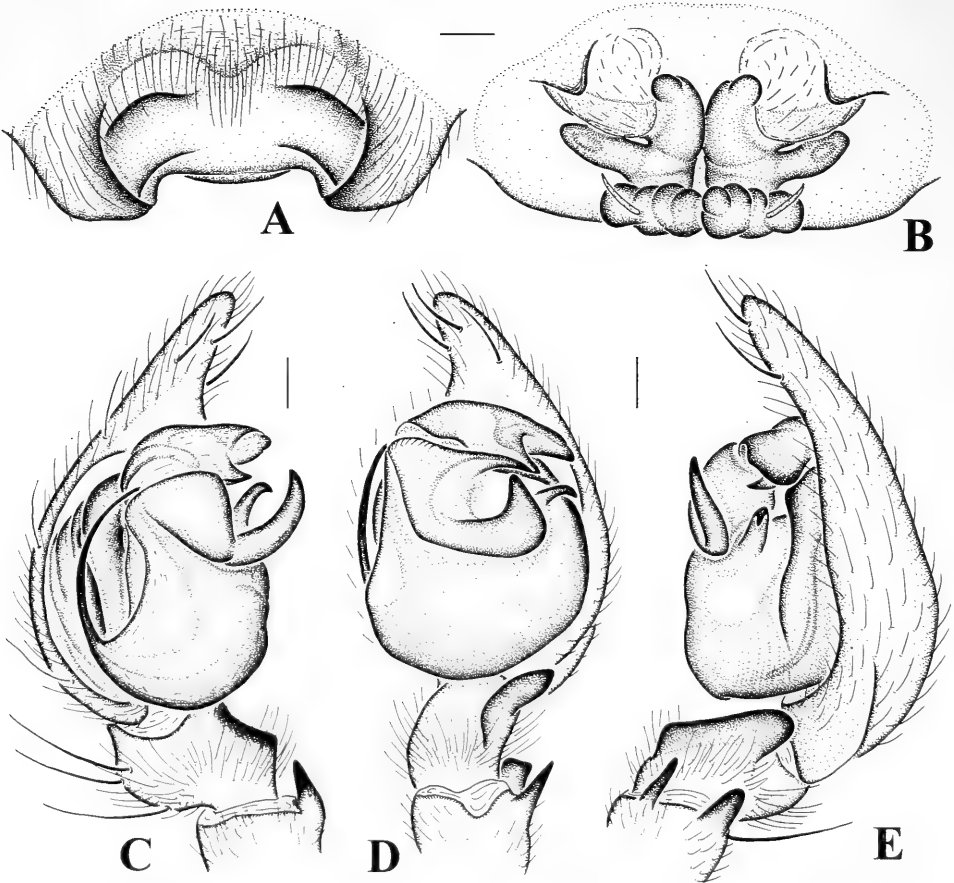


FIGURE 3. *Coronilla gemata* Wang. A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view; E. Pedipalpus, retrolateral view.

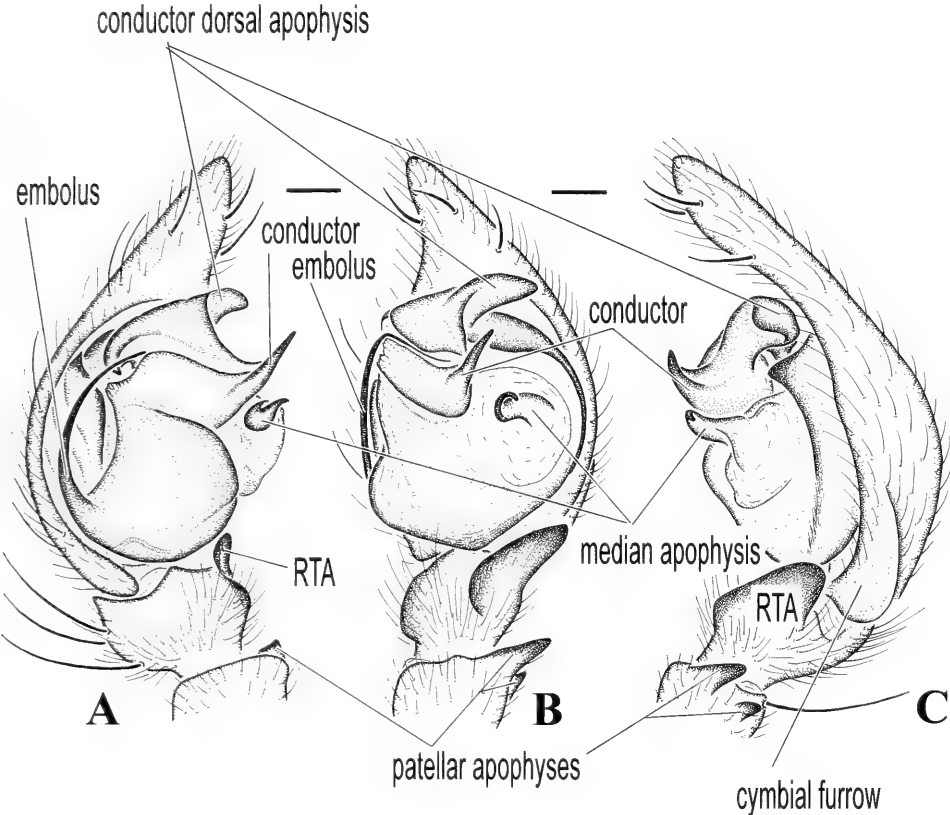


FIGURE 4. *Coronilla libo* Wang, sp. nov. A. Pedipalpus, prolateral view, B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

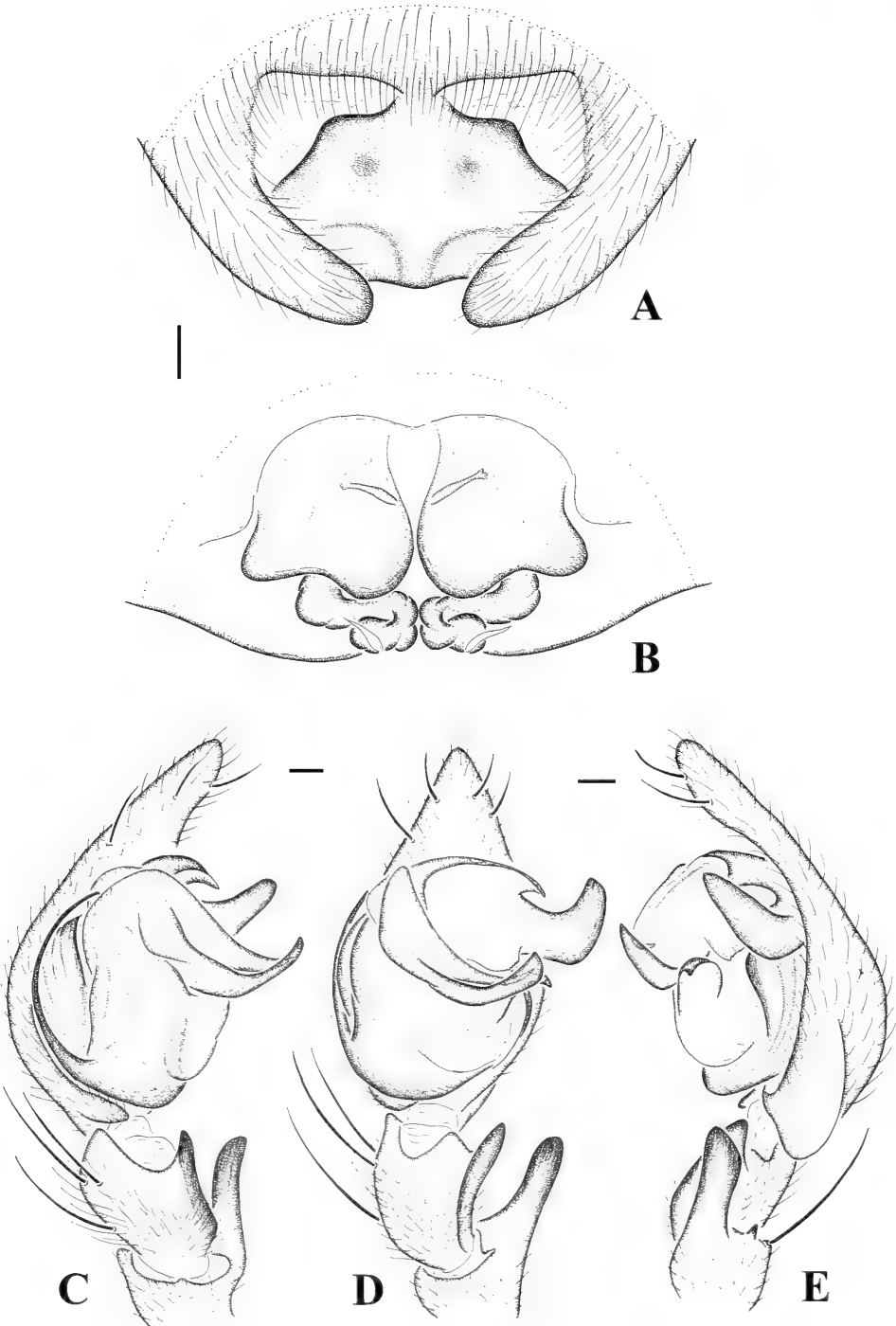


FIGURE 5. *Coronilla sigillata* Wang. A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

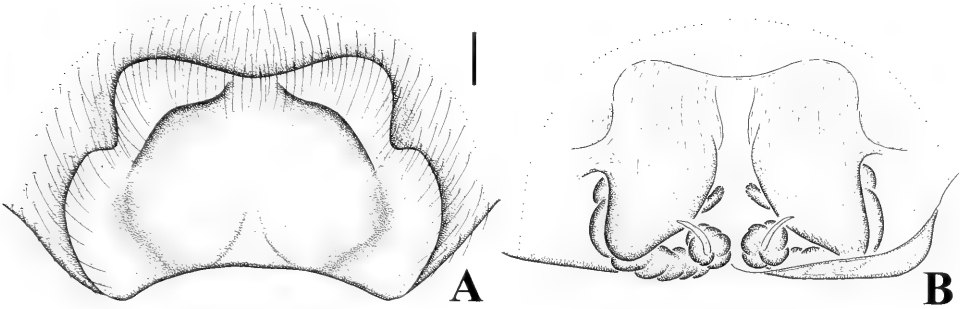


FIGURE 6. *Coronilla subsigillata* Wang, sp. nov. A. Epigynum. B. Vulva.

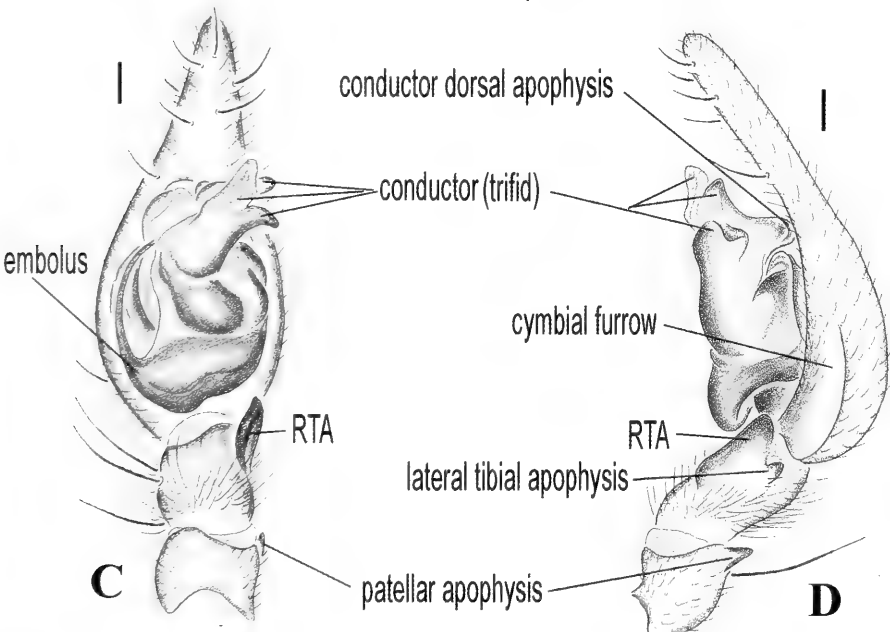
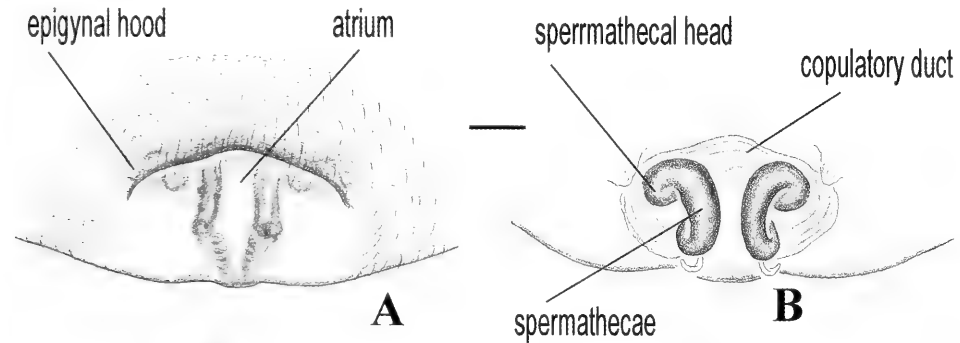


FIGURE 7. *Draconarius absentis* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

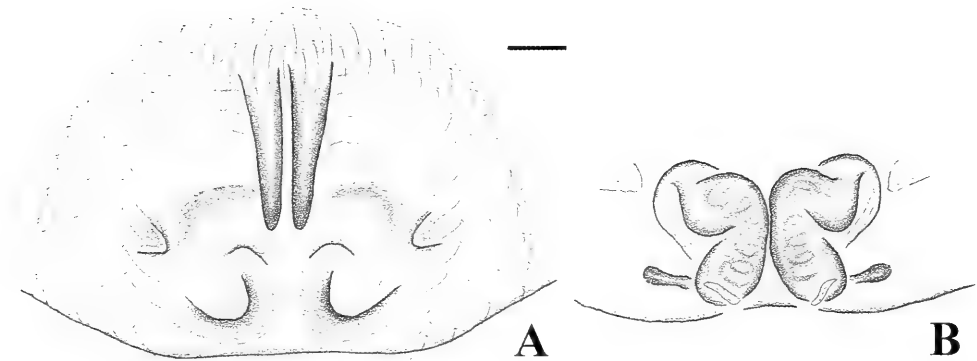


FIGURE 8. *Draconarius acidentatus* (Peng and Yin). A. Epigynum. B. Vulva.

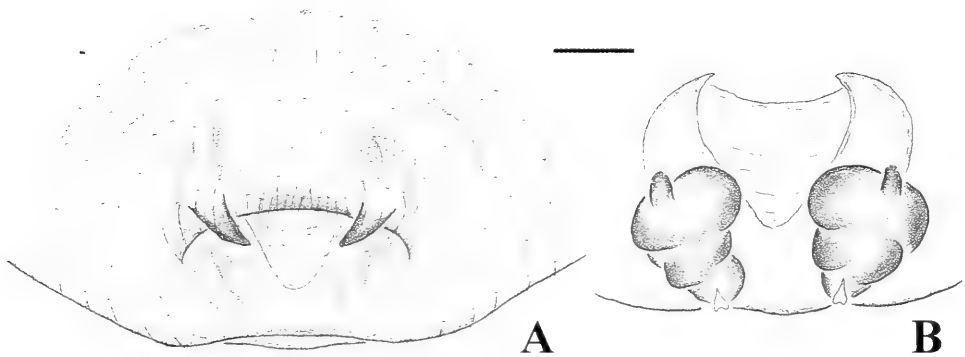


FIGURE 9. *Draconarius adligansus* (Peng and Yin). A. Epigynum. B. Vulva.



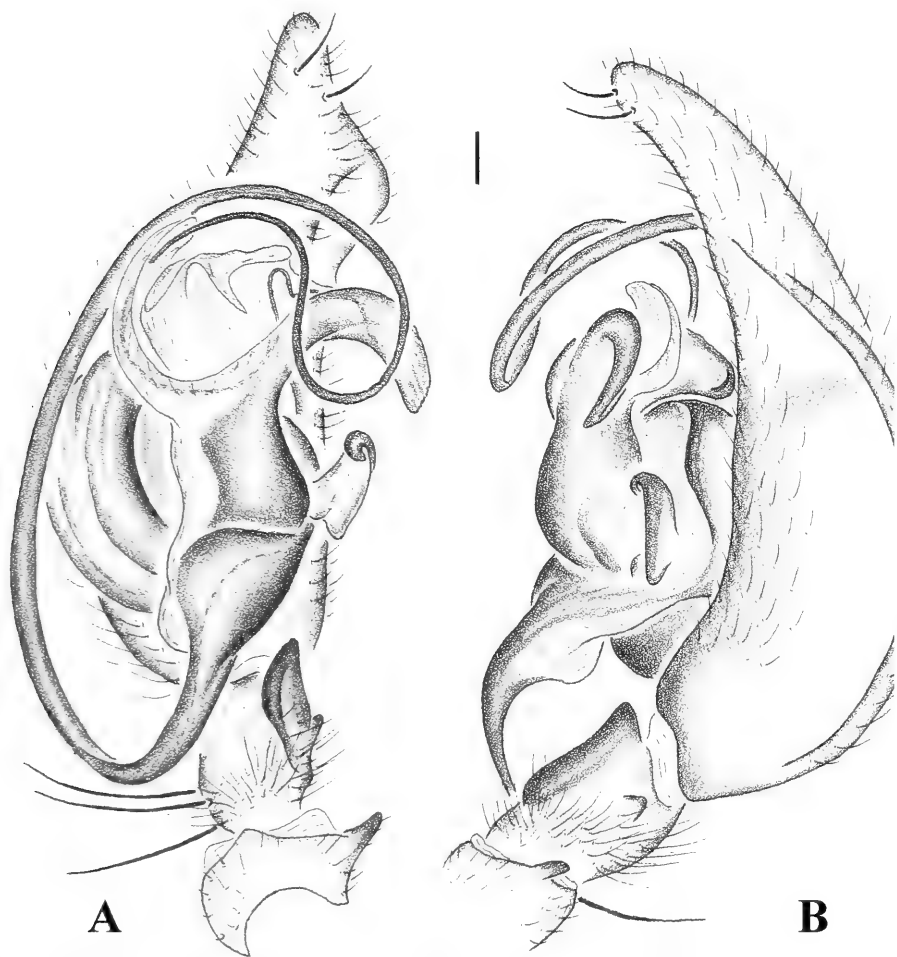


FIGURE 10. *Draconarius agrestis* Wang, sp. nov. A. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view.

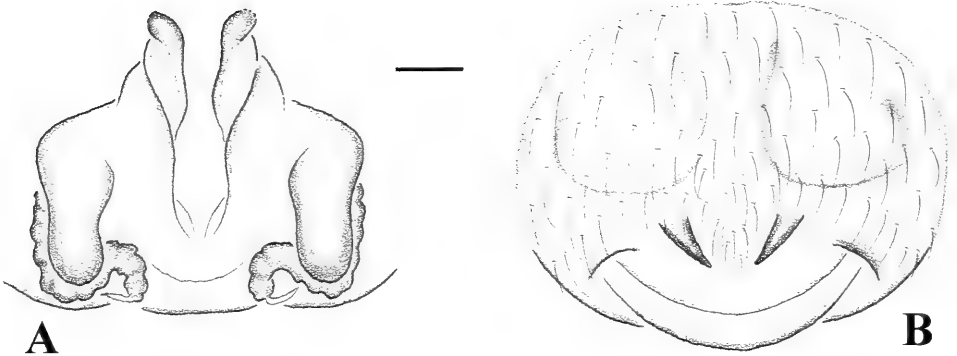


FIGURE 11. *Draconarius arcuatus* Wang. sp. nov. A. Vulva. B. Epigynum.

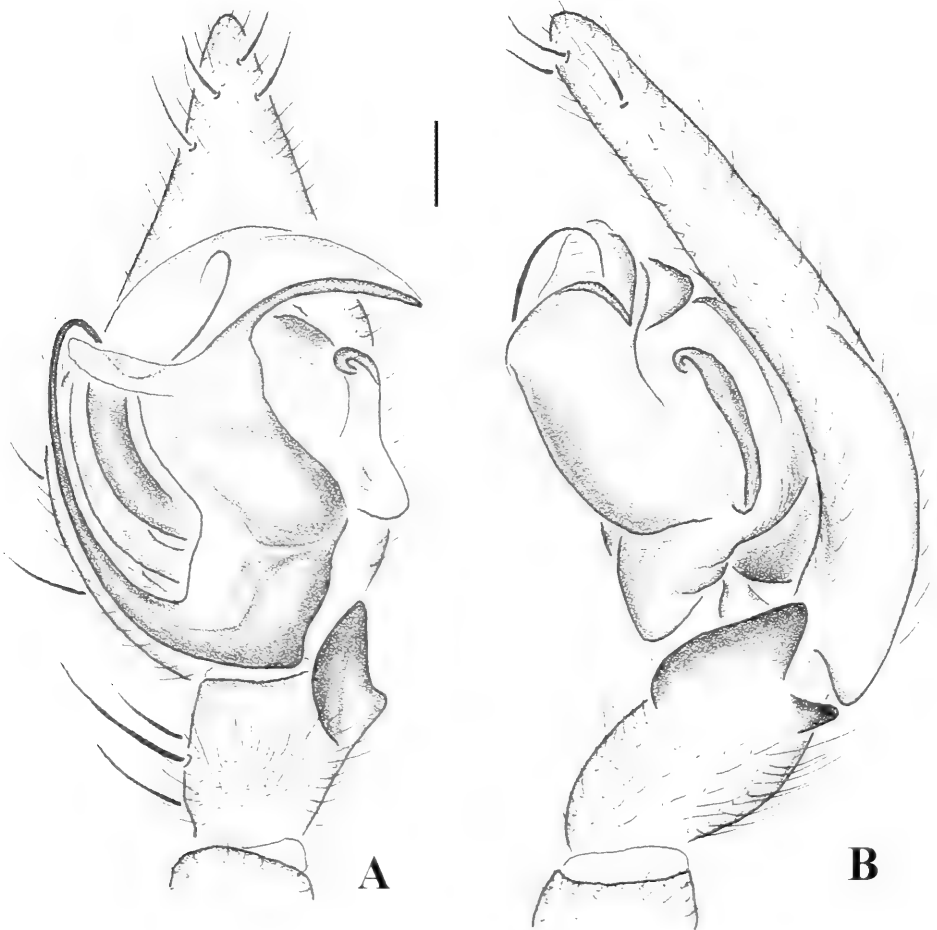


FIGURE 12. *Draconarius argenteus* Wang. sp. nov. A. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view.

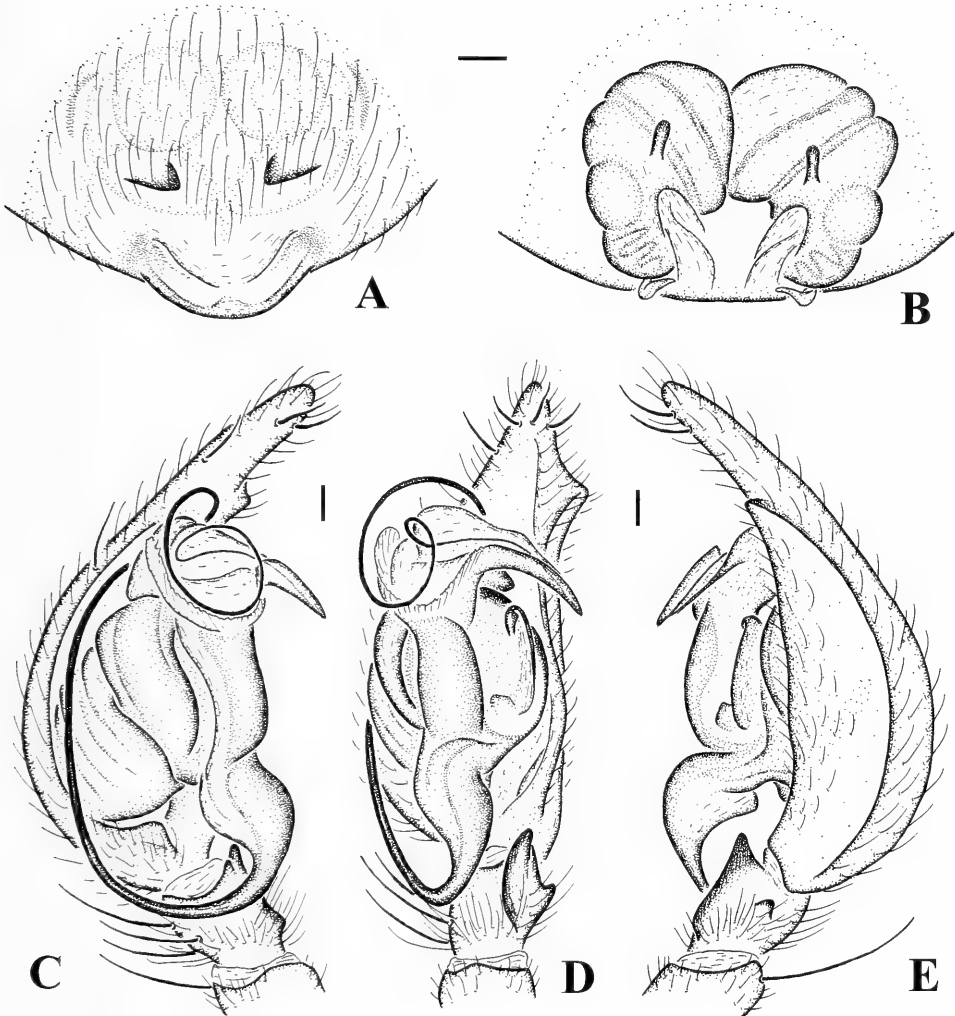


FIGURE 13. *Draconarius aspinatus* (Wang et al.). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

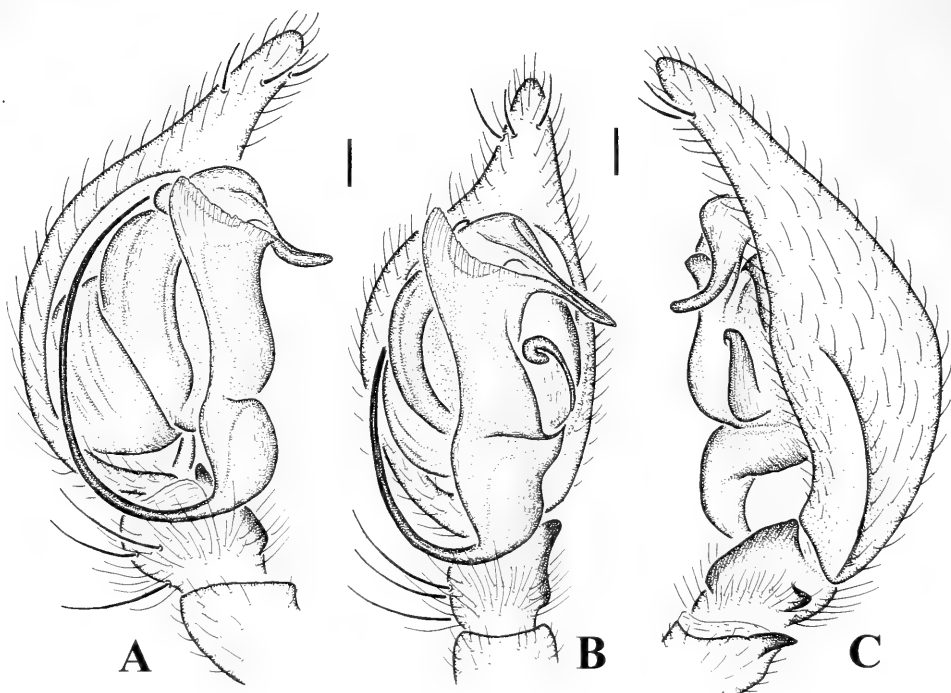


FIGURE 14. *Draconarius baronii* (Brignoli). A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

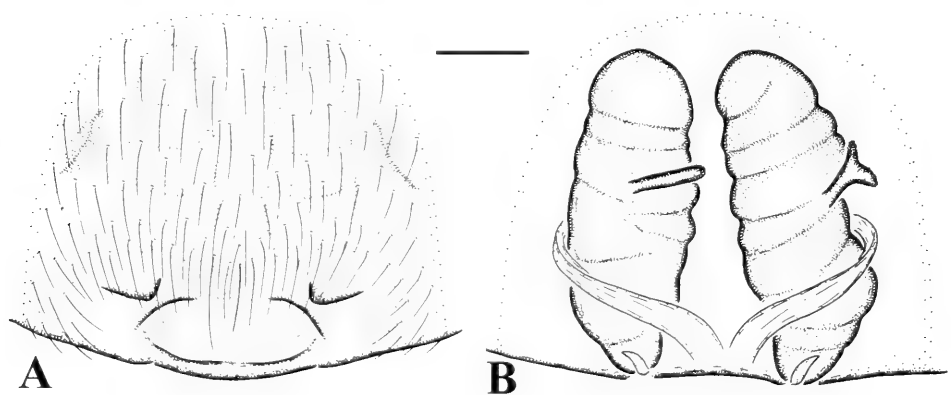


FIGURE 15. *Draconarius baxiantaiensis* Wang, sp. nov. A. Epigynum. B. Vulva.

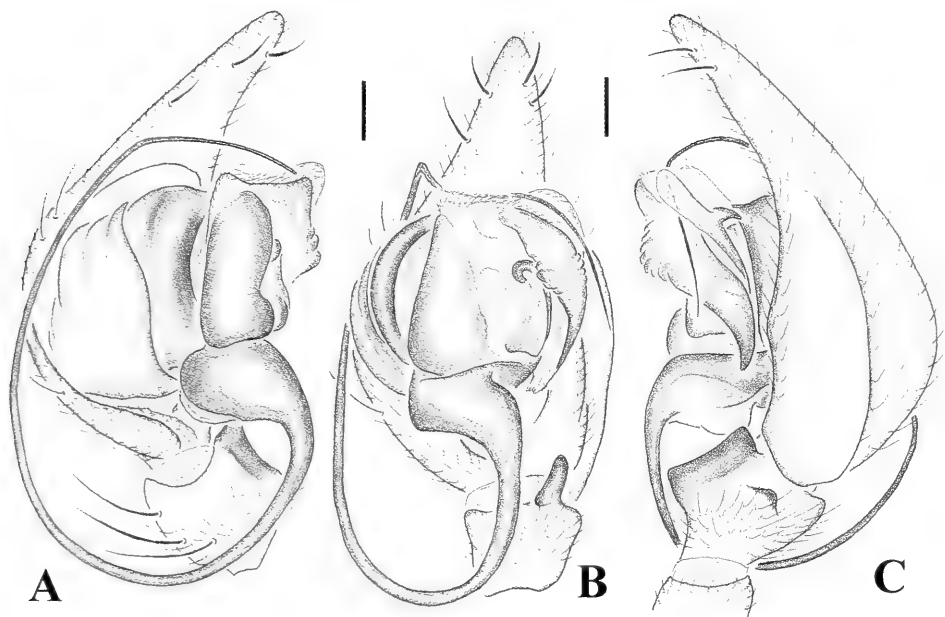


FIGURE 16. *Draconarius bituberculatus* (Wang et al.). A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

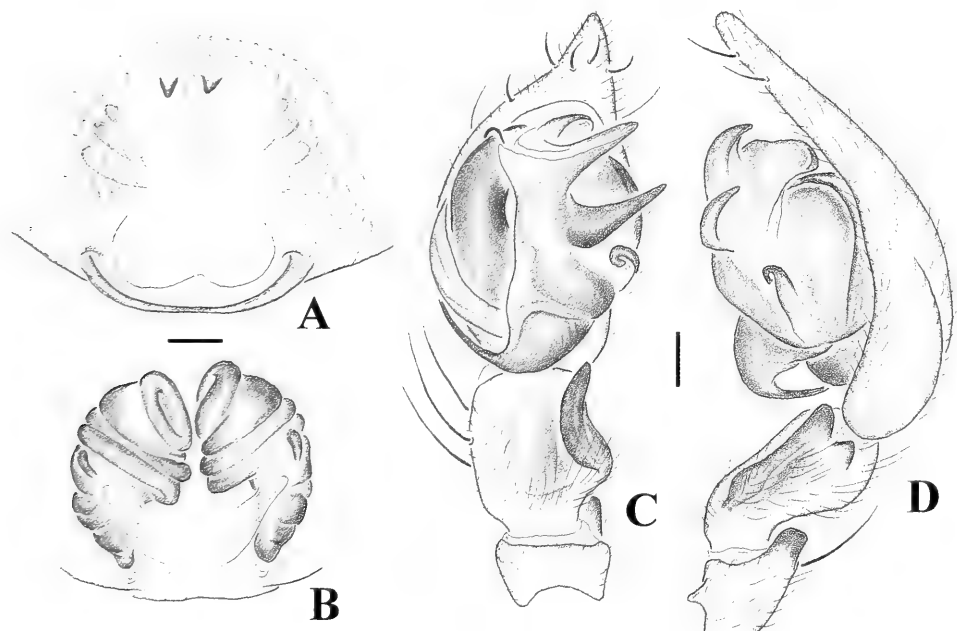


FIGURE 17. *Draconarius calcariformis* (Wang). A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

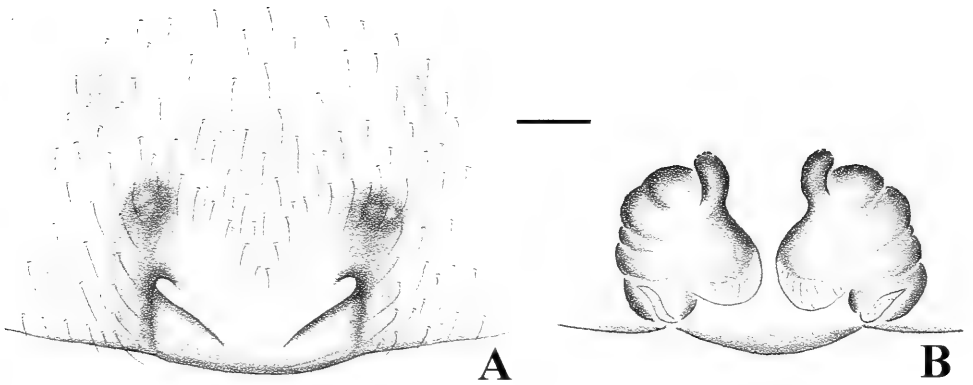


FIGURE 18. *Draconarius capitulatus* Wang, sp. nov. A. Epigynum. B. Vulva.

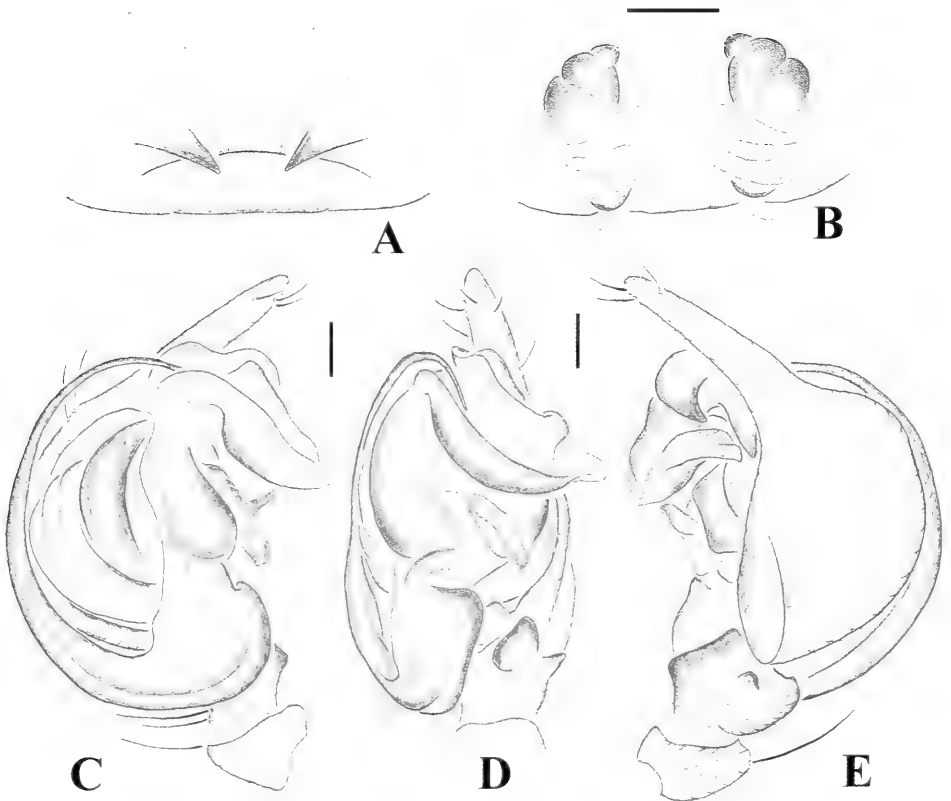


FIGURE 19. *Draconarius carinatus* (Wang et al.). A. Epigynum. B. Vulva. C. pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

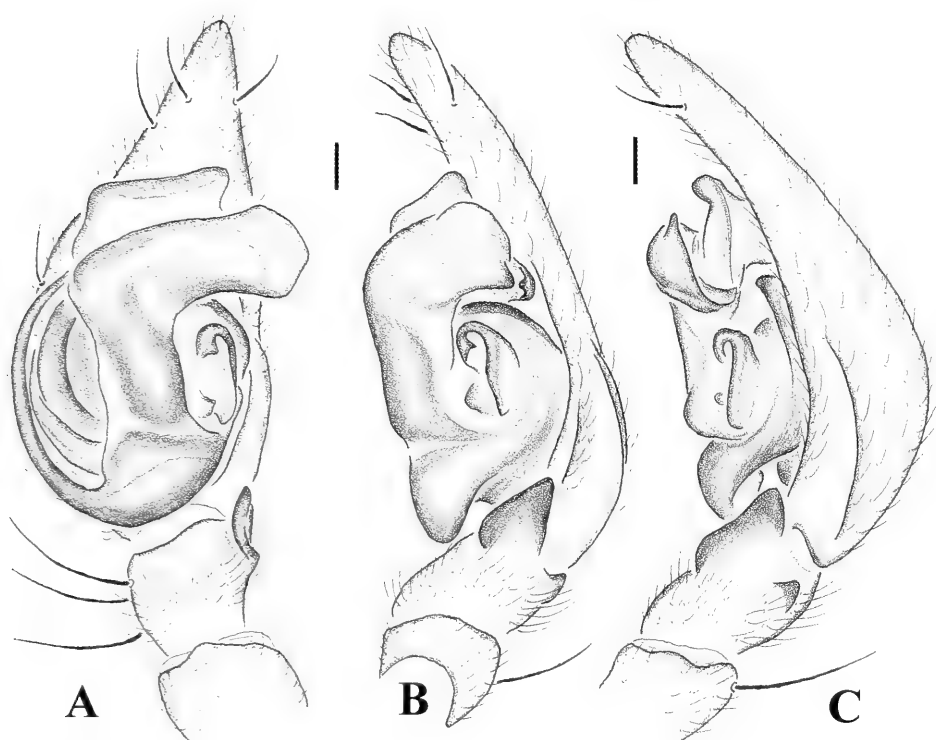


FIGURE 20. *Draconarius chaiqiaoensis* (Zhang, Peng and Kim). A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

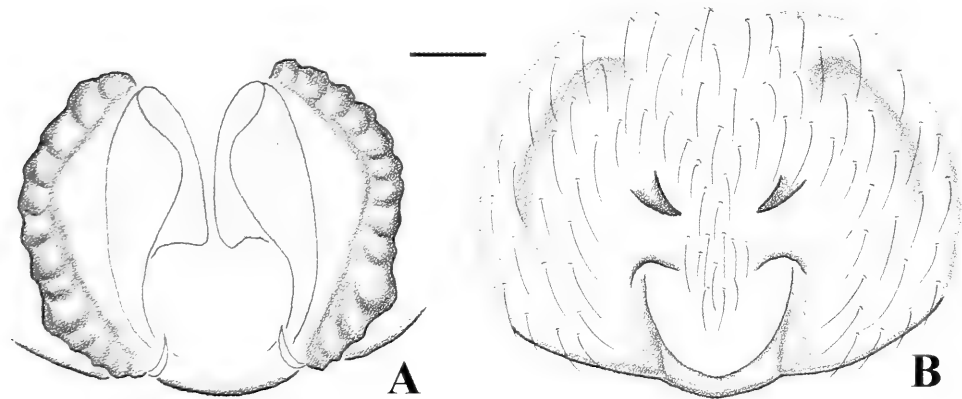


FIGURE 21. *Draconarius cheni* (Platnick). A. Vulva. B. Epigynum.

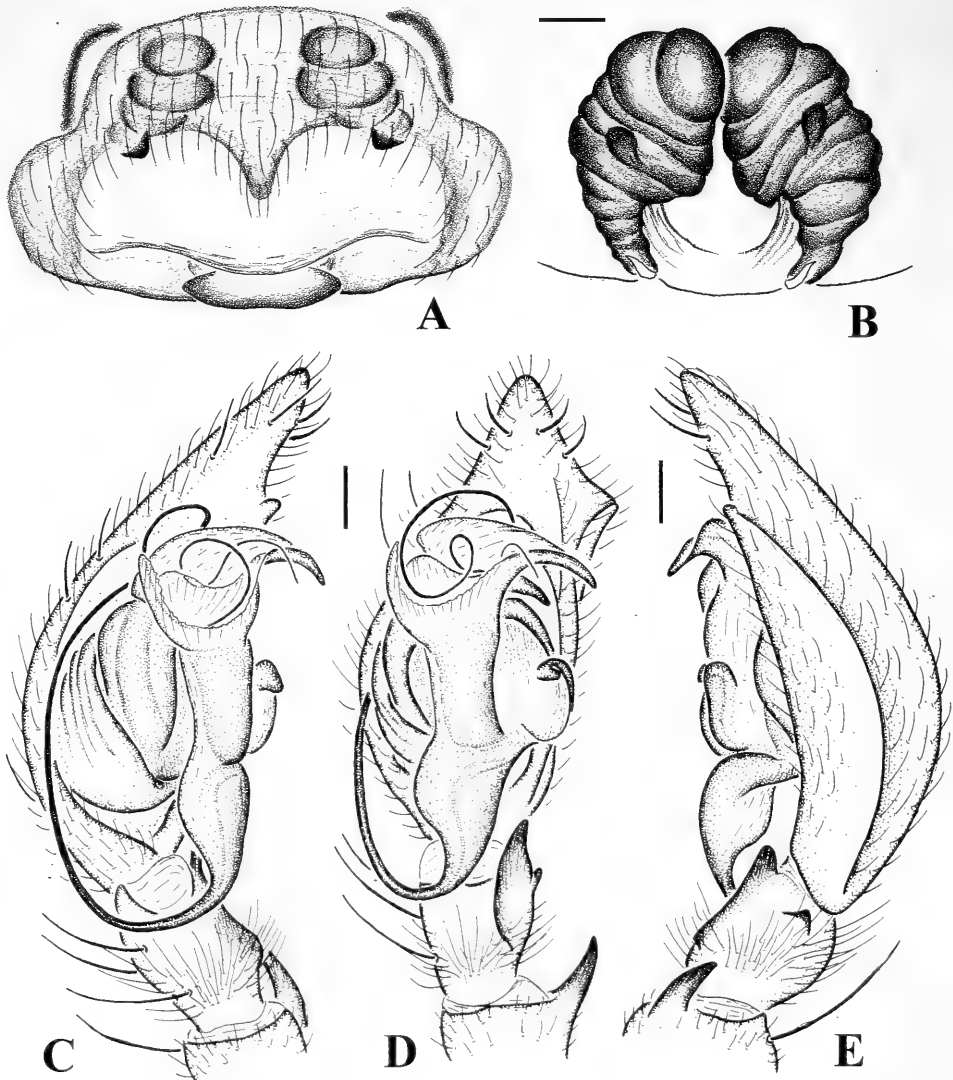


FIGURE 22. *Coelotes coreanus* (Paik and Yaginuma). A. Epigynum. B. Vulva. C. pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.



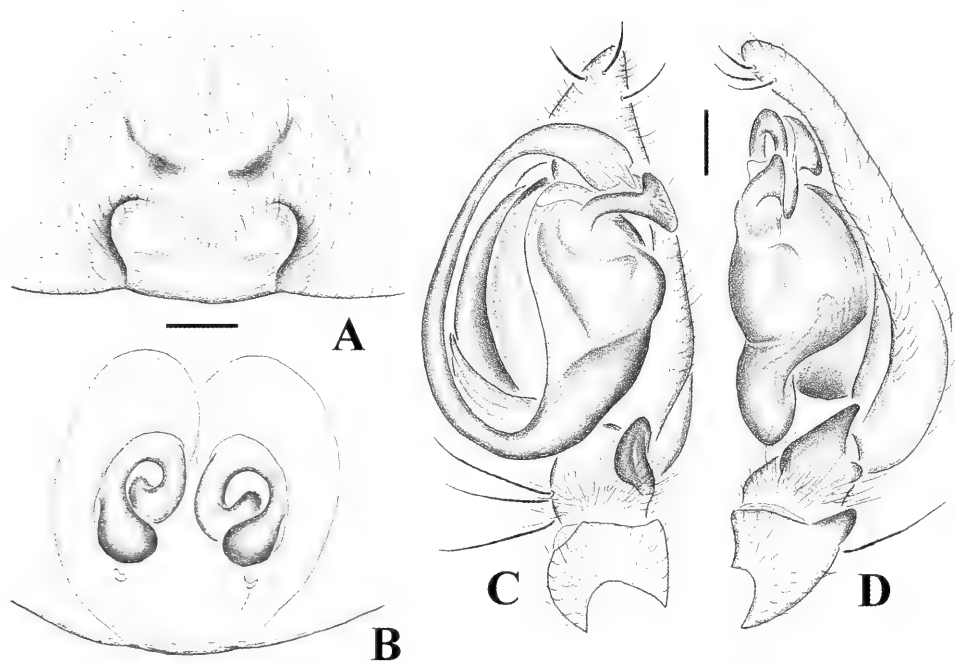


FIGURE 23. *Draconarius curiosus* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

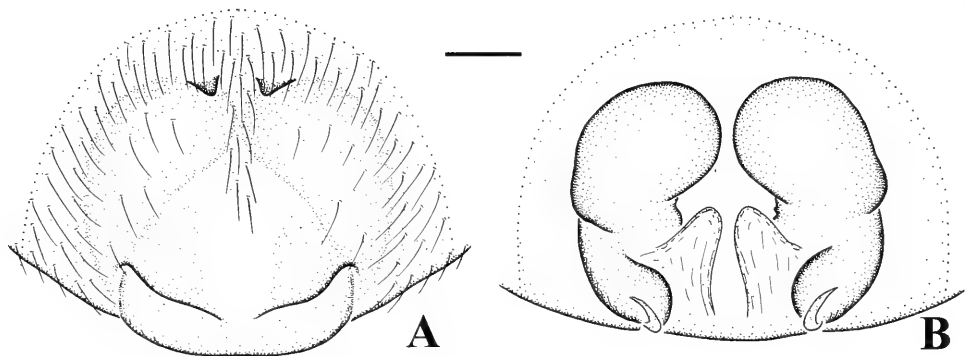


FIGURE 24. *Draconarius davidi* (Schenkel). A. Epigynum. B. Vulva.

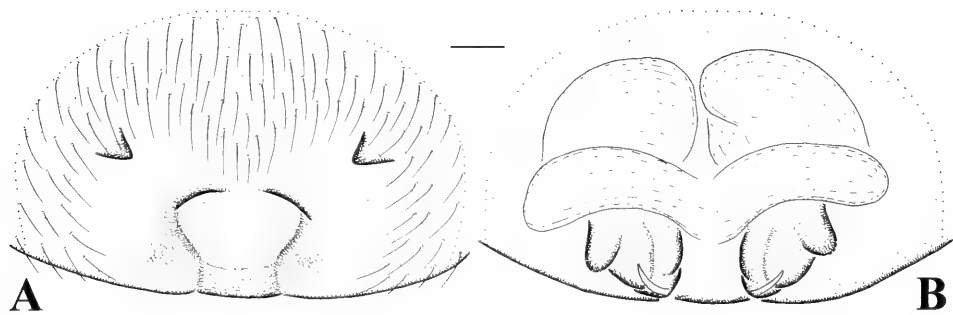


FIGURE 25. *Draconarius denisi* (Schenkel). A. Epigynum. B. Vulva.

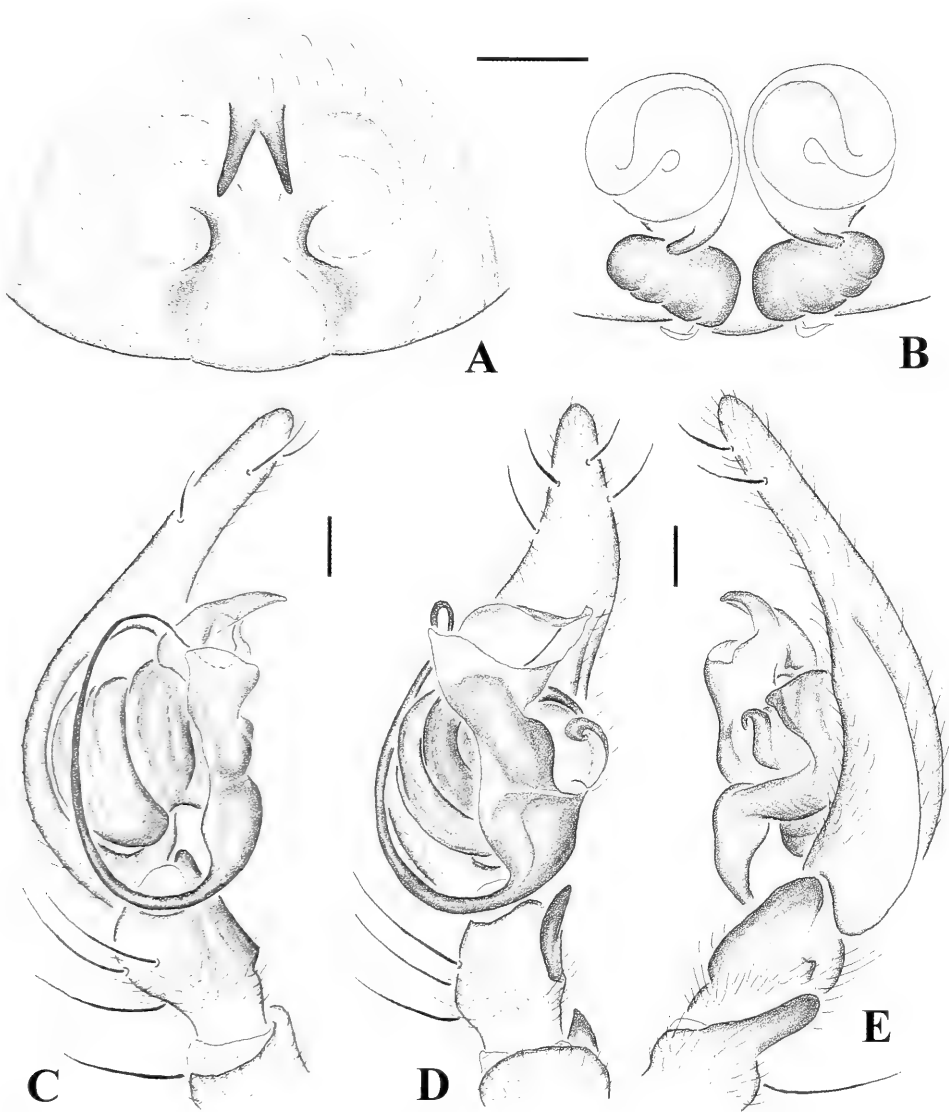


FIGURE 26. *Draconarius digitusiformis* (Wang et al.). A. Epigynum. B. Vulva. C. padipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

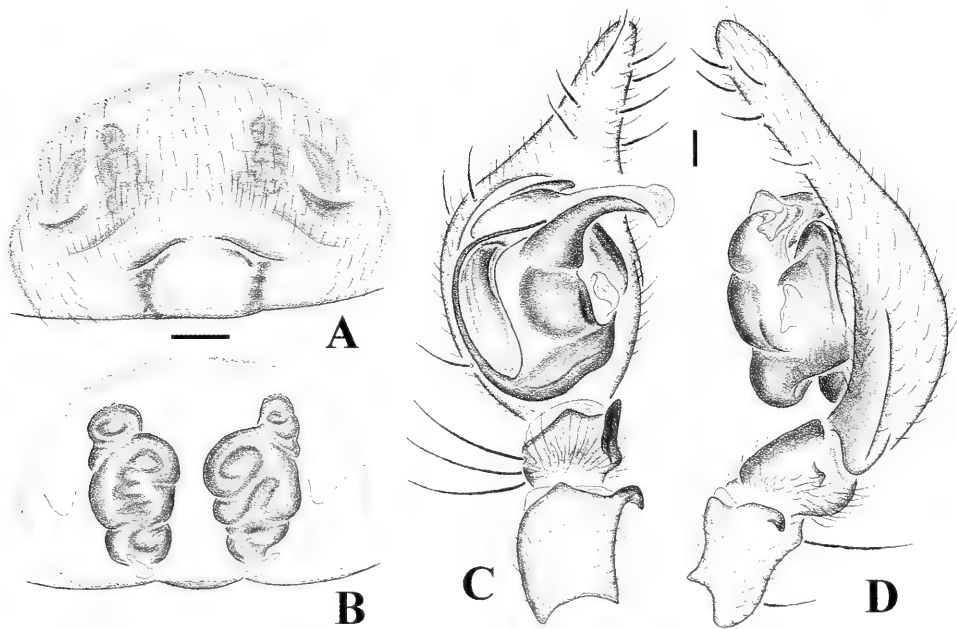


FIGURE 27. *Draconarius disgregus* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

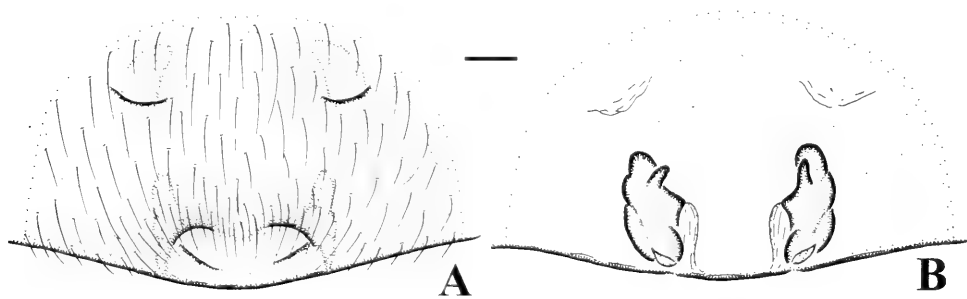


FIGURE 28. *Draconarius dissitus* Wang, sp. nov. A. Epigynum. B. Vulva.

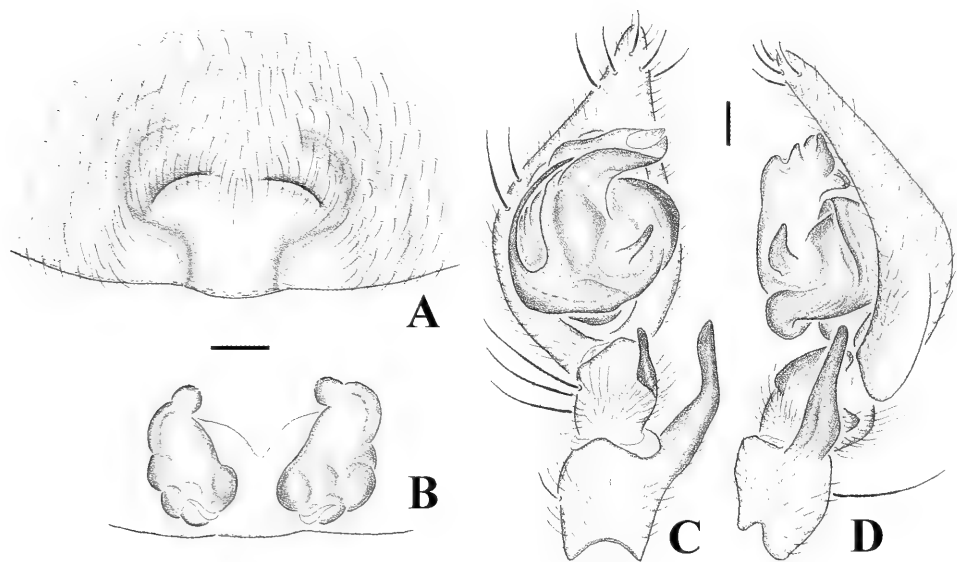


FIGURE 29. *Draconarius dubius* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

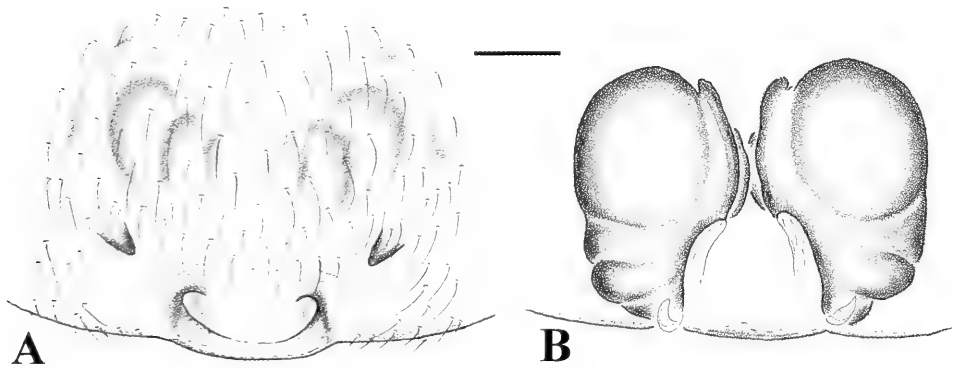


FIGURE 30. *Draconarius episomos* Wang, sp. nov. A. Epigynum. B. Vulva.

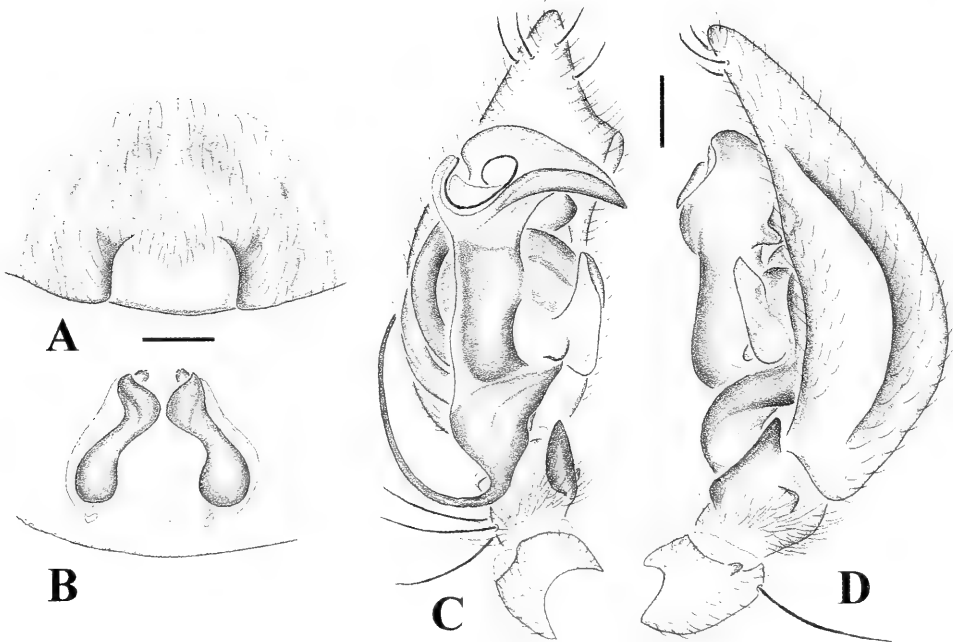


FIGURE 31. *Draconarius griswoldi* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

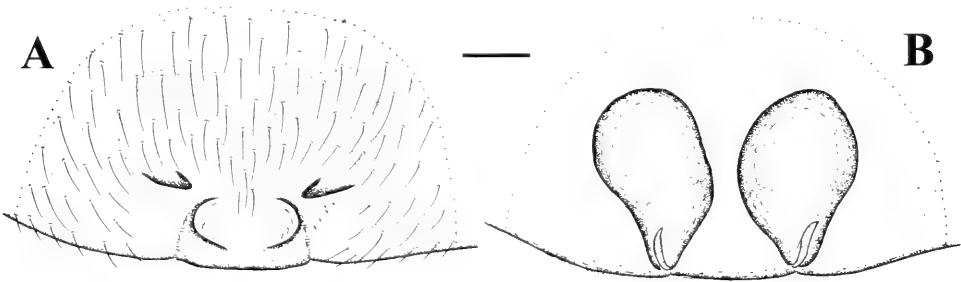


FIGURE 32. *Draconarius gorkha* (Brignoli). A. Epigynum. B. Vulva.

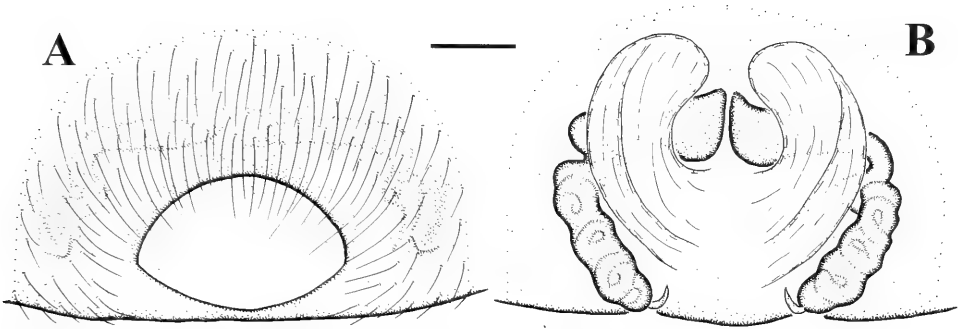


FIGURE 33. *Draconarius haopingensis* Wang, sp. nov. A. Epigynum. B. Vulva.

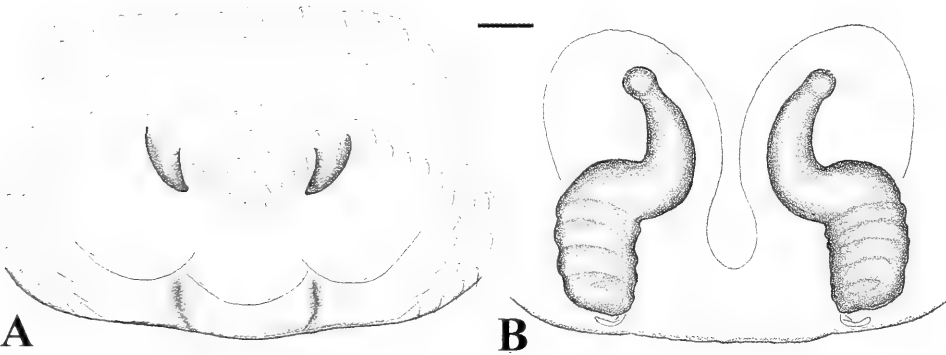


FIGURE 34. *Draconarius hangzhouensis* (Chen). A. Epigynum. B. Vulva.

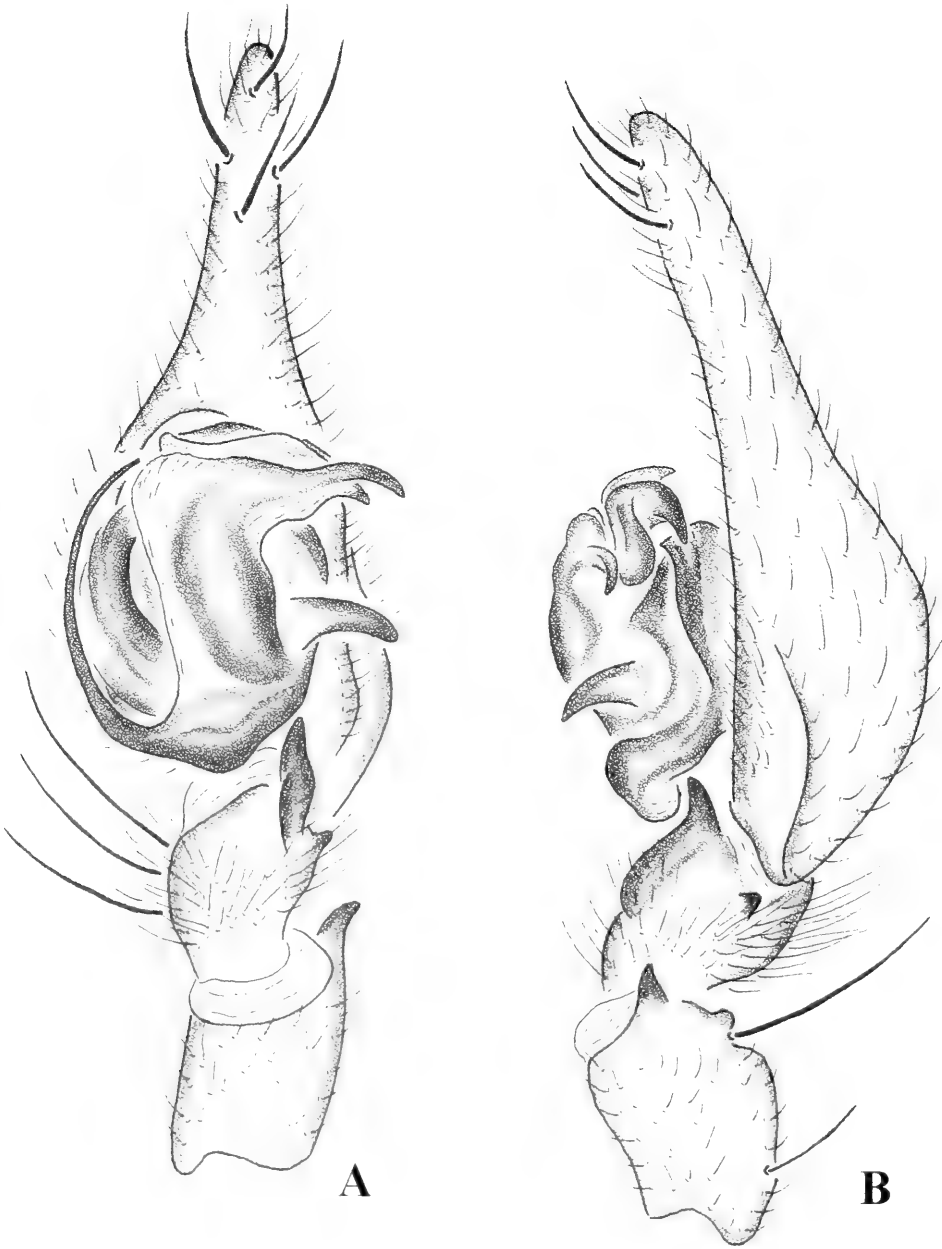


FIGURE 35. *Draconarius incertus* Wang, sp. nov. A. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view.



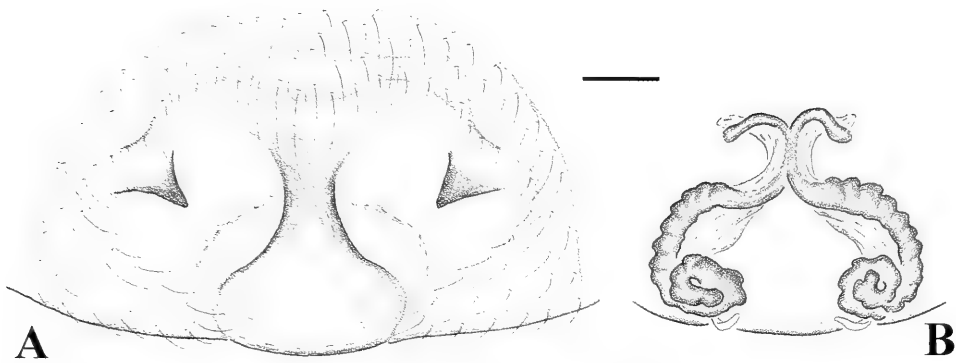


FIGURE 36. *Draconarius jiangyongensis* (Peng, Gong and Kim). A. Epigynum. B. Vulva.

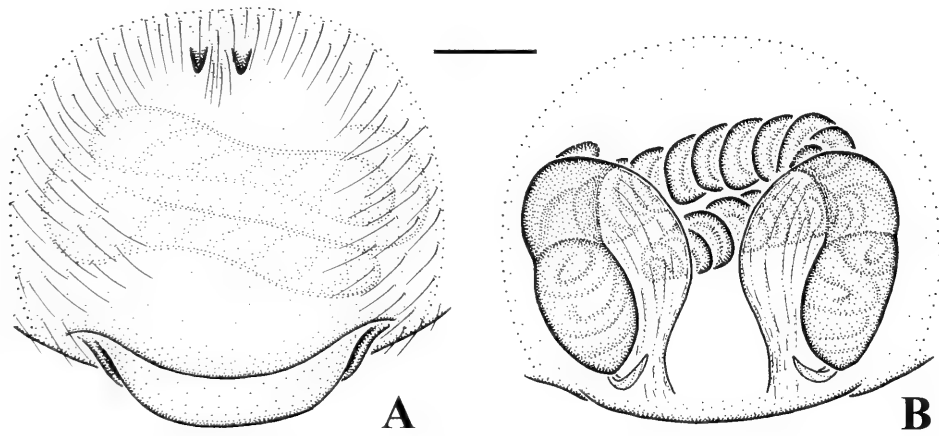


FIGURE 37. *Draconarius labiatus* (Wang and Ono). A. Epigynum. B. Vulva.



FIGURE 38. *Draconarius linxiaensis* Wang, sp. nov. A. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view.

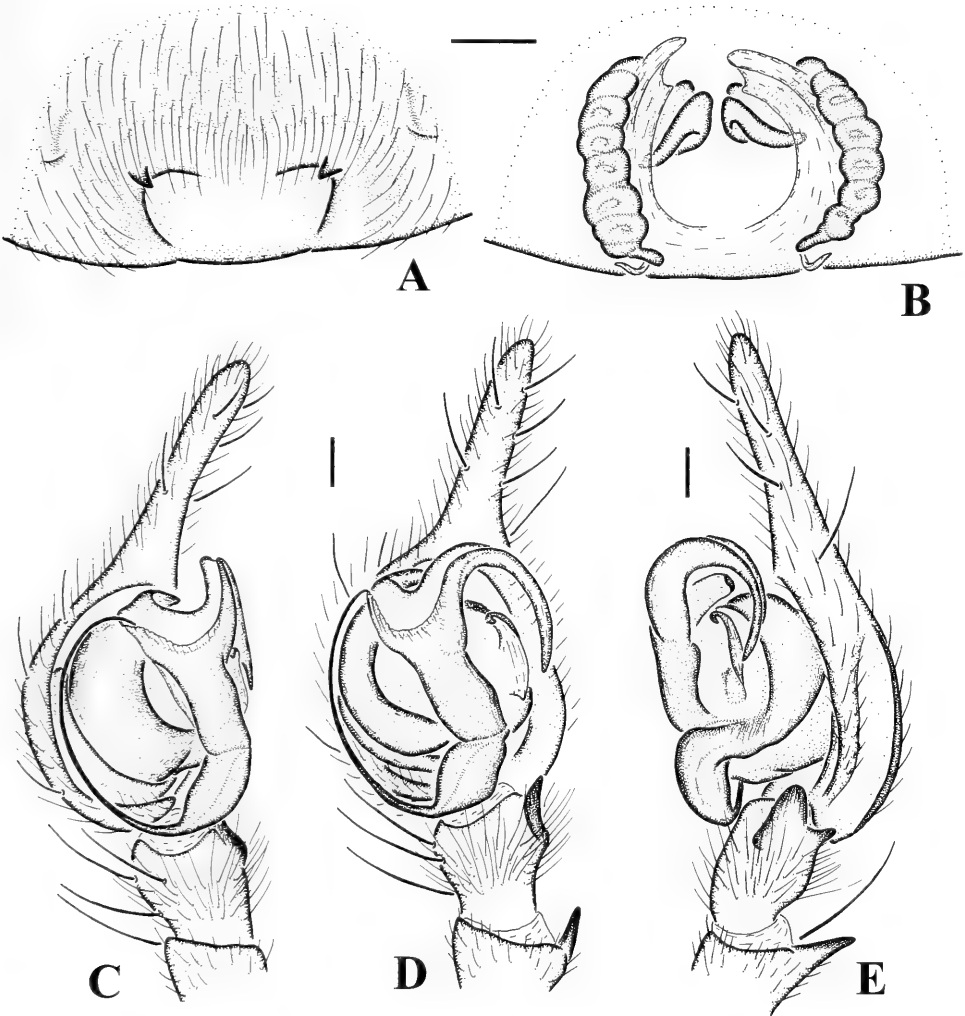


FIGURE 39. *Draconarius lutulentus* (Wang et al.), types. A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

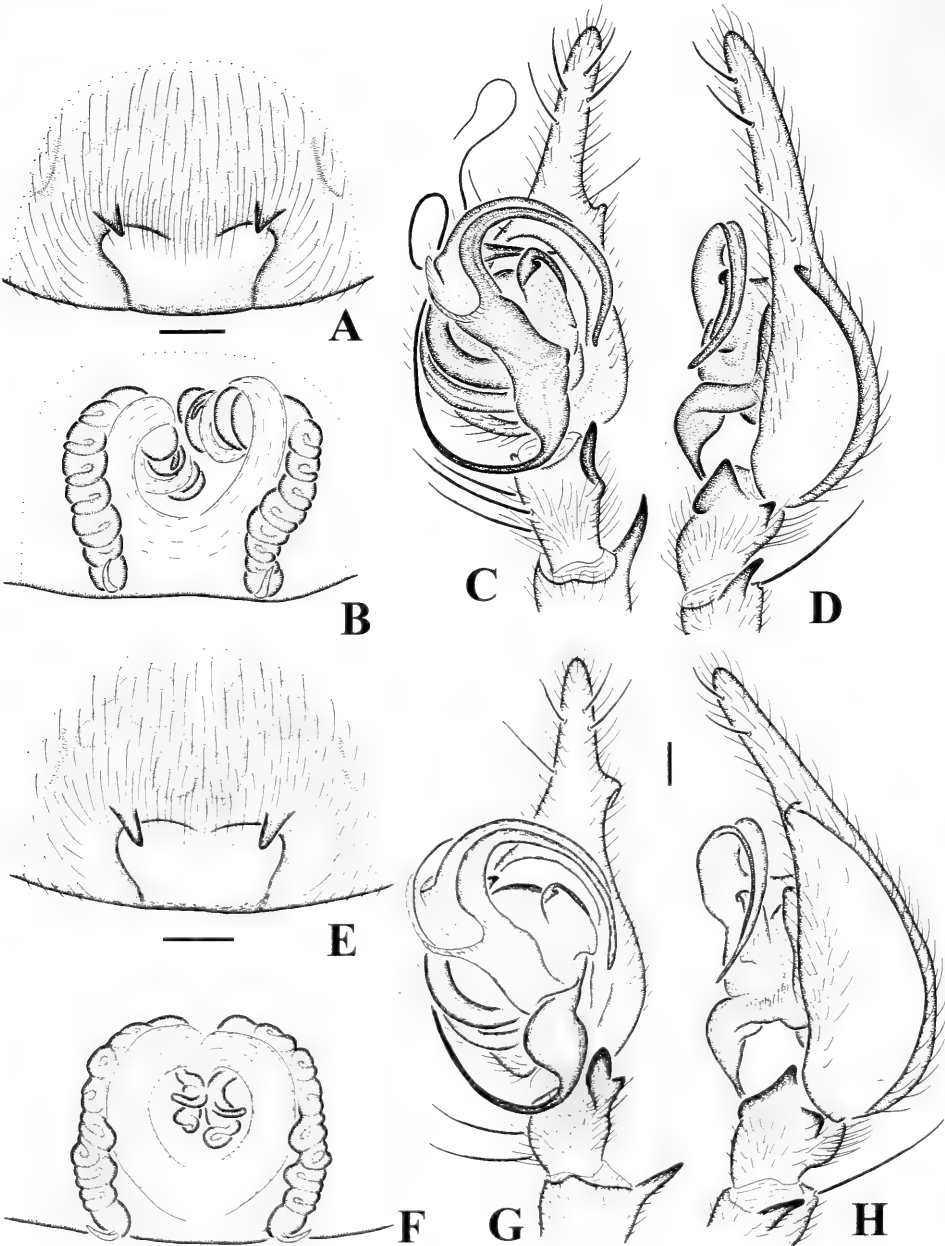


FIGURE 40. *Draconarius lutulentus* (Wang et al.), showing genitalic variations: A-D from Wudangshan, Hubei, China; E-H from Hongping, Hubei, China. A, E. Epigynum. B, F. Vulva. C, G. Pedipalpus, ventral view. D, H. Pedipalpus, retro-lateral view.

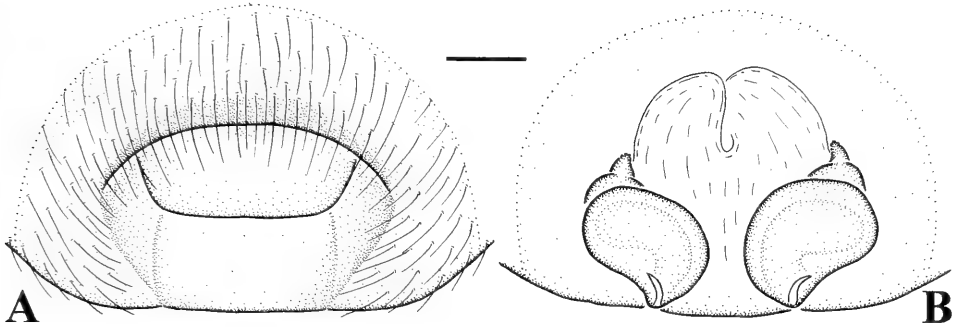


FIGURE 41. *Draconarius magniceps* (Schenkel). A. Epigynum. B. Vulva.

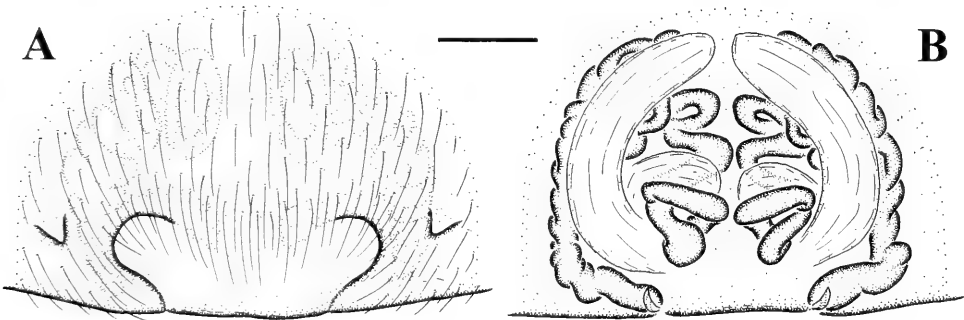


FIGURE 42. *Draconarius molluscus* (Wang et al.). A. Epigynum. B. Vulva.

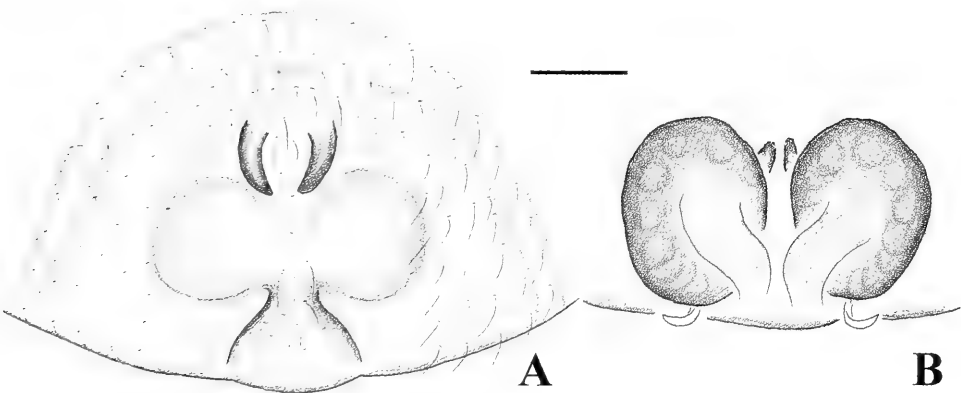


FIGURE 43. *Draconarius nanyuensis* (Peng and Yin). A. Epigynum. B. Vulva.

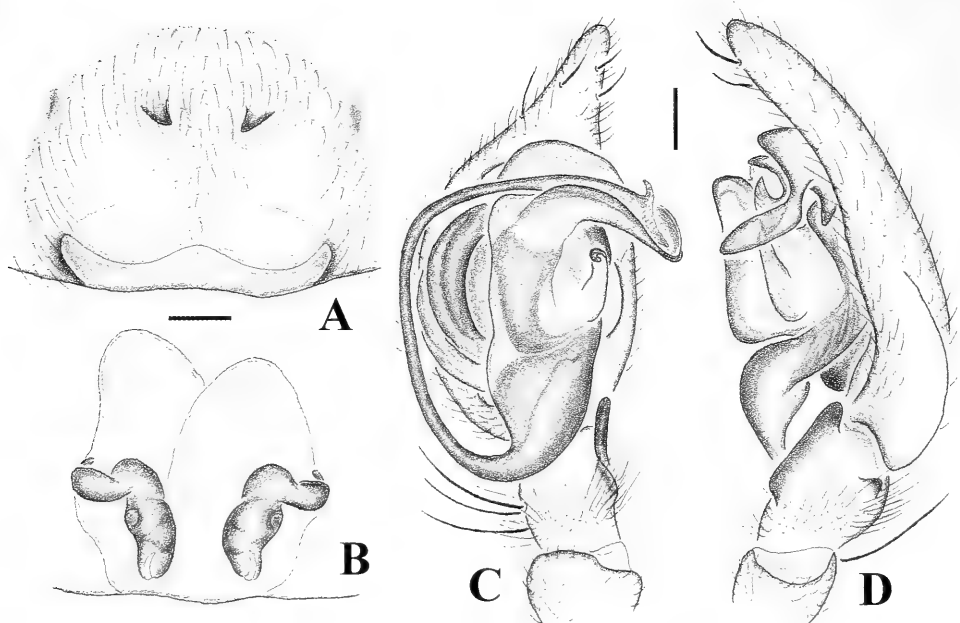


FIGURE 44. *Draconarius neixiangensis* (Hu, Wang and Wang). A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

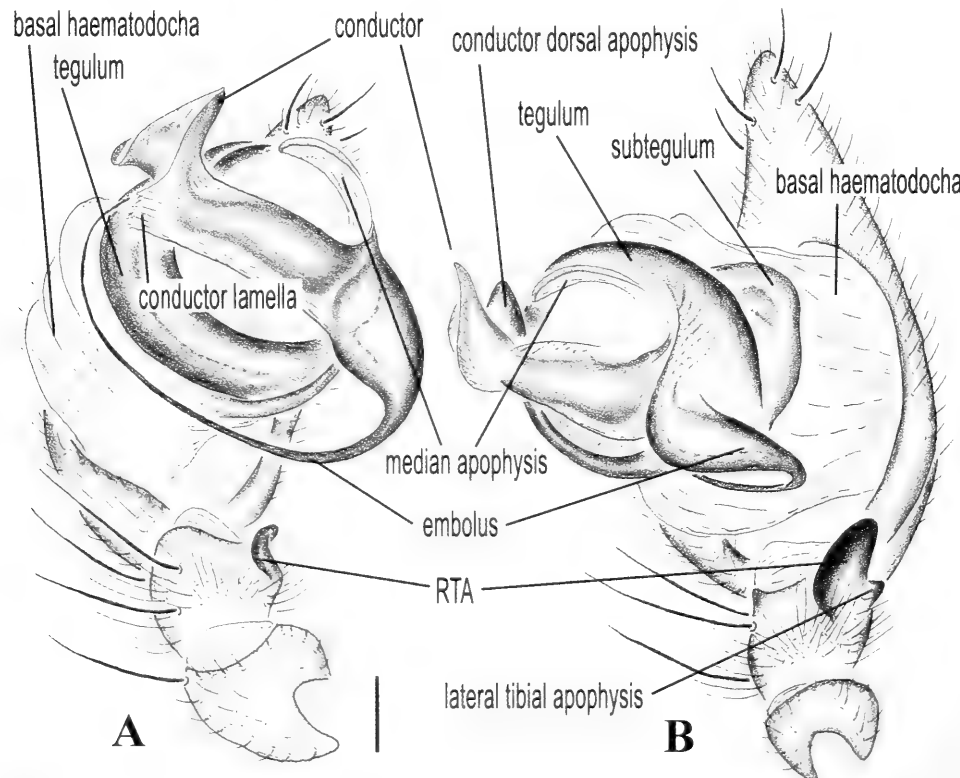


FIGURE 45. *Draconarius nudulus* Wang, sp. nov. A. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view. (Haematodochae slightly expanded).

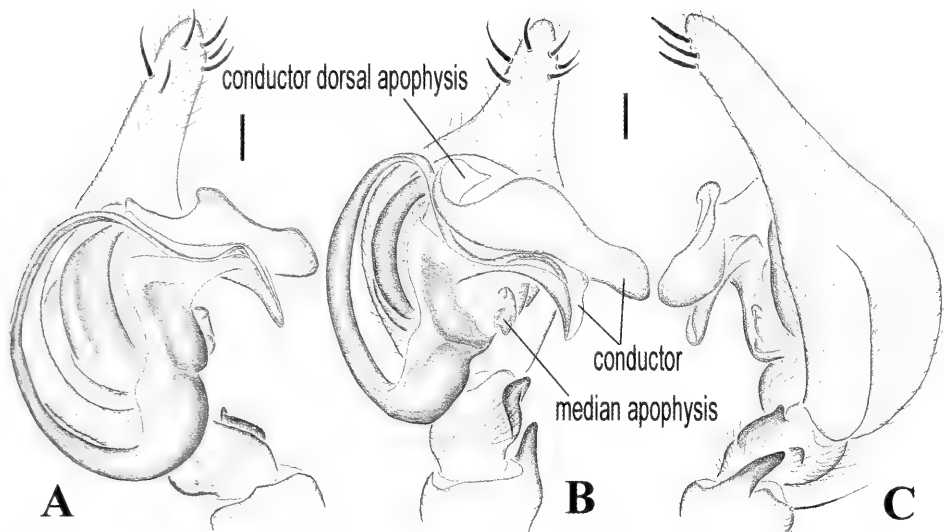


FIGURE 46. *Draconarius ornatus* (Wang et al.). A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view.

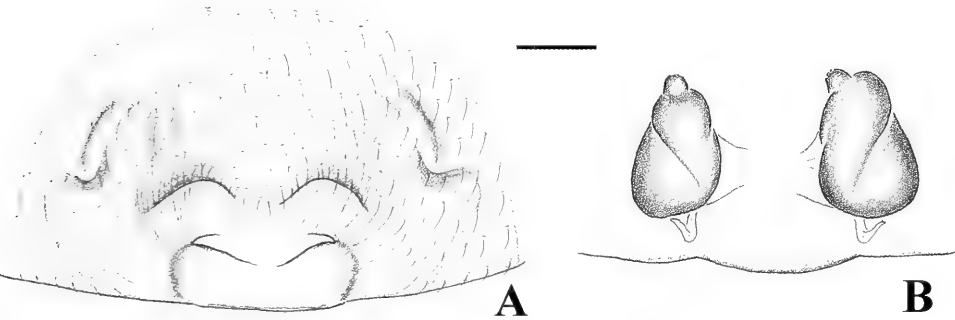


FIGURE 47. *Draconarius parabruneus* Wang, sp. nov. A. Epigynum. B. Vulva.

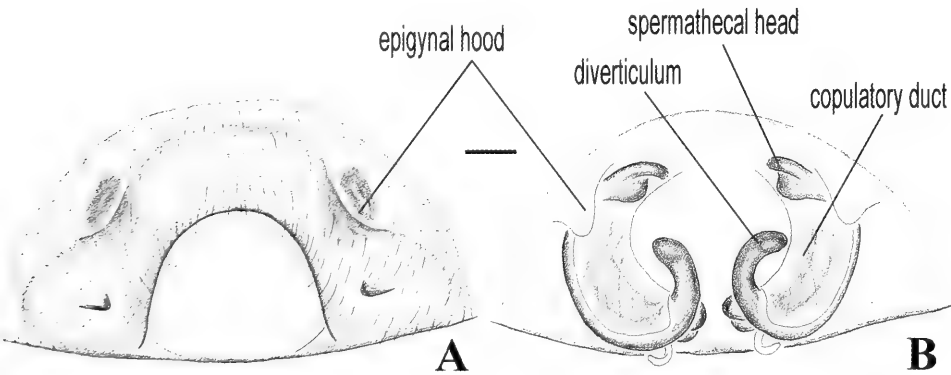


FIGURE 48. *Draconarius paraterebratus* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

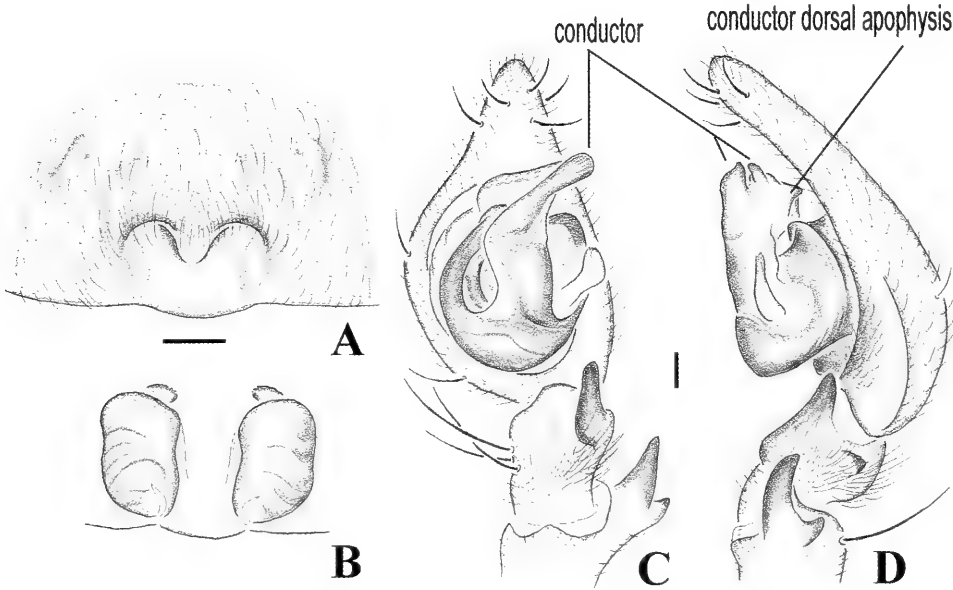


FIGURE 49. *Draconarius patellabifidus* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.



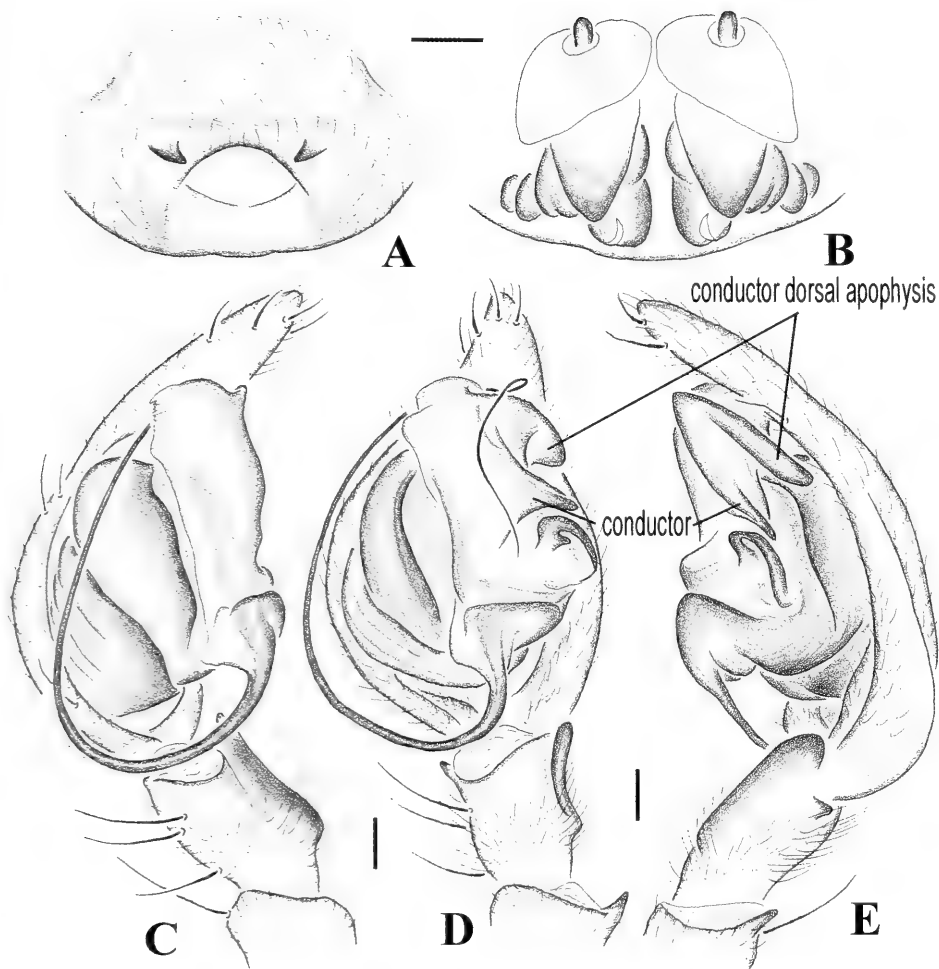


FIGURE 50. *Draconarius penicillatus* (Wang et al.). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

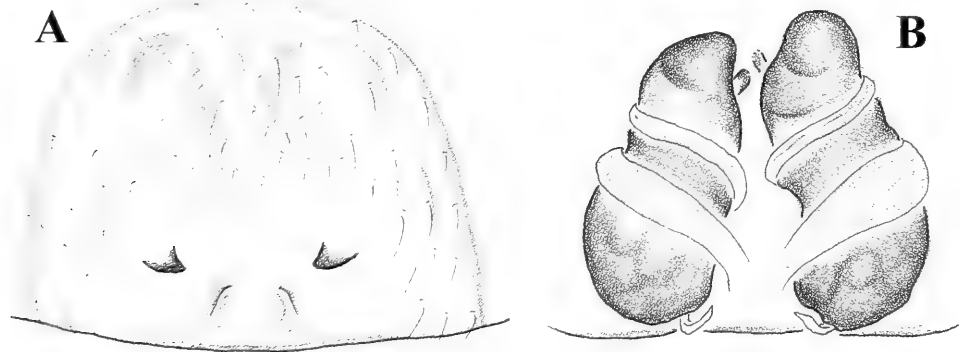


FIGURE 51. *Draconarius potanini* (Schenkel). A. Epigynum. B. Vulva.

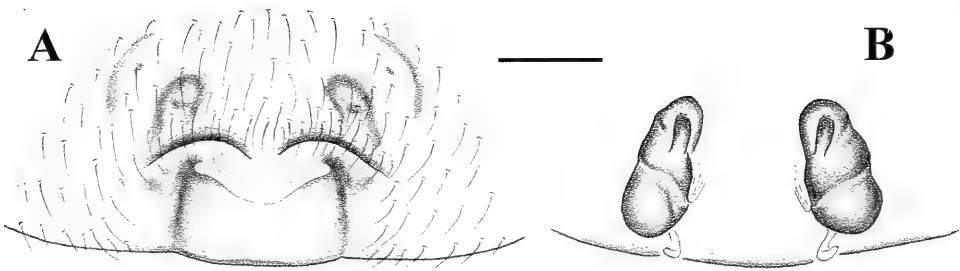


FIGURE 52. *Draconarius pseudobrunneus* Wang, sp. nov. A. Epigynum. B. Vulva.

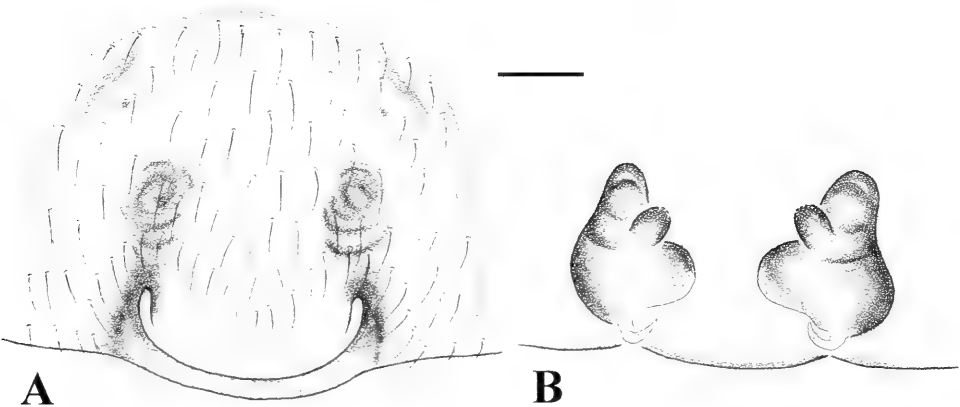


FIGURE 53. *Draconarius pseudocapitulatus* Wang, sp. nov. A. Epigynum. B. Vulva.

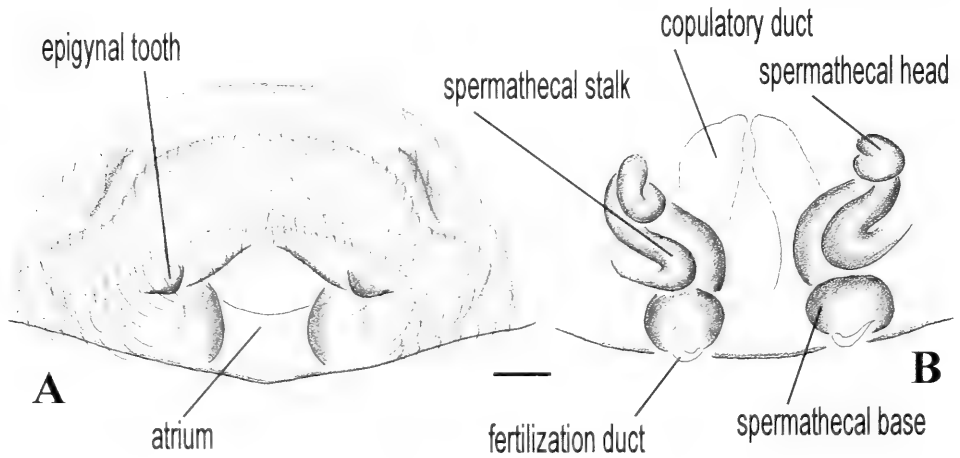


FIGURE 54. *Draconarius pseudowuermlii* Wang, sp. nov. A. Epigynum. B. Vulva.

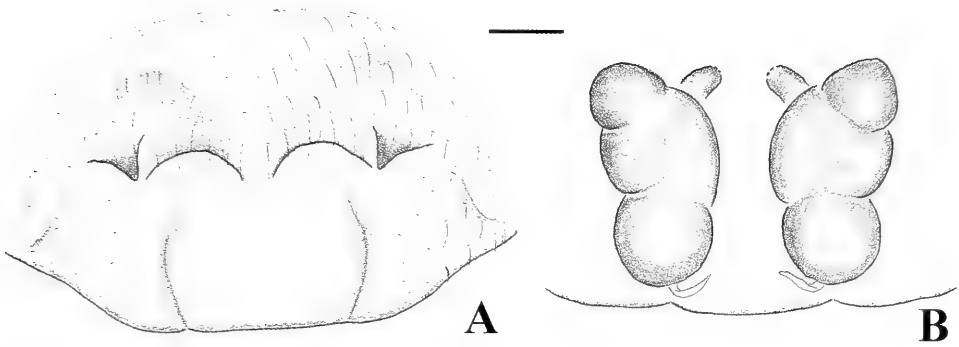


FIGURE 55. *Draconarius quadratus* (Wang et al.). A. Epigynum. B. Vulva.

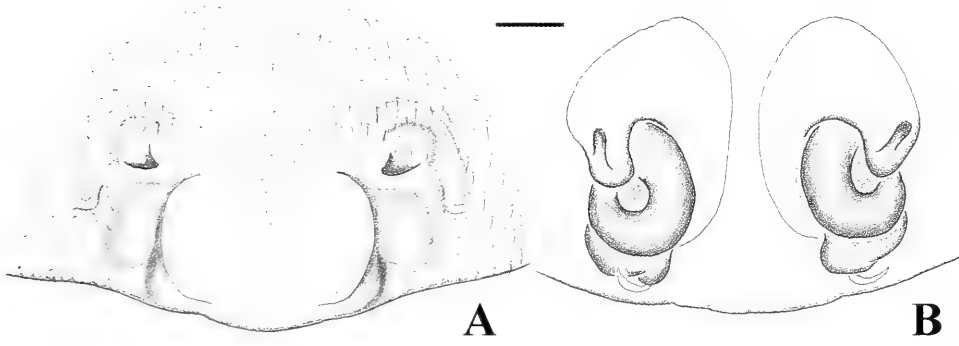


FIGURE 56. *Draconarius rotundus* Wang, sp. nov. A. Epigynum. B. Vulva.

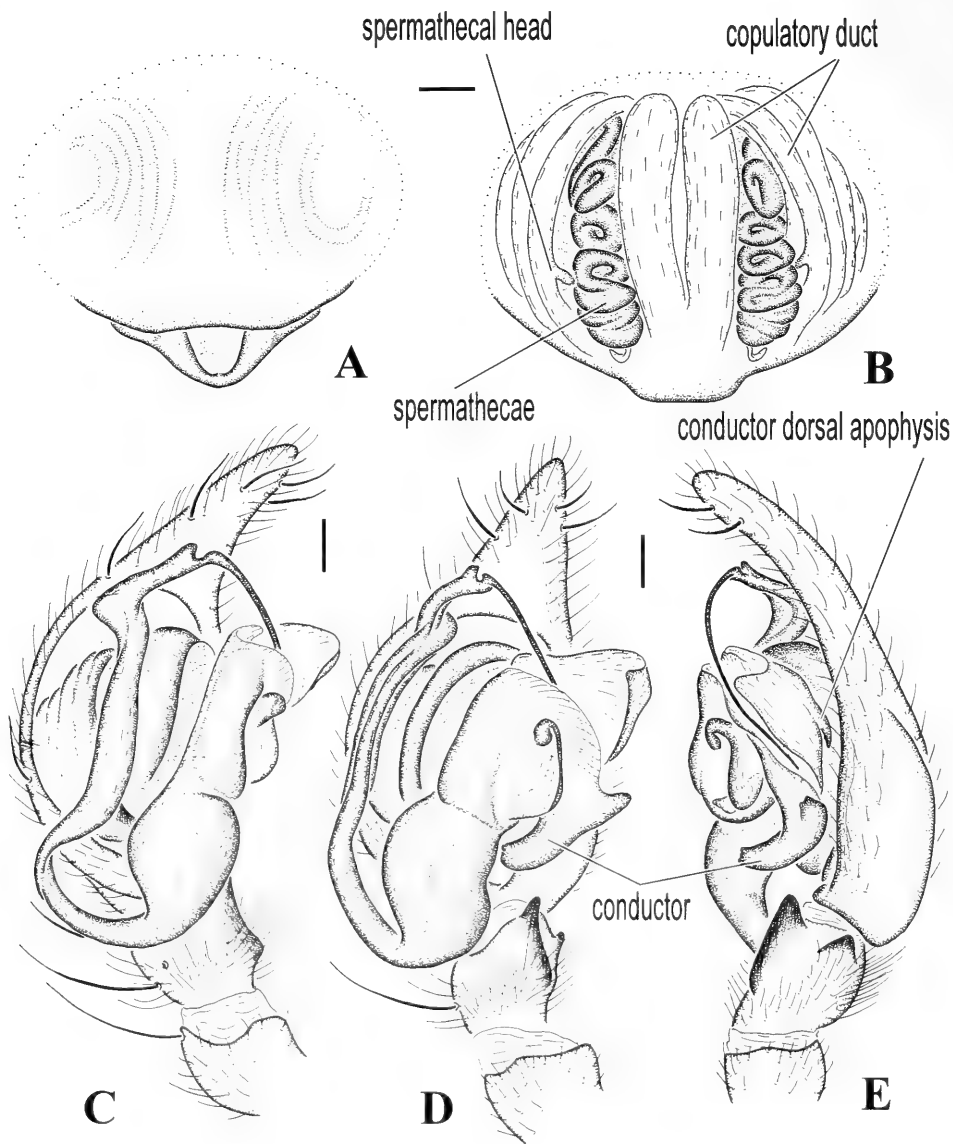


FIGURE 57. *Draconarius rufulus* (Wang et al.). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

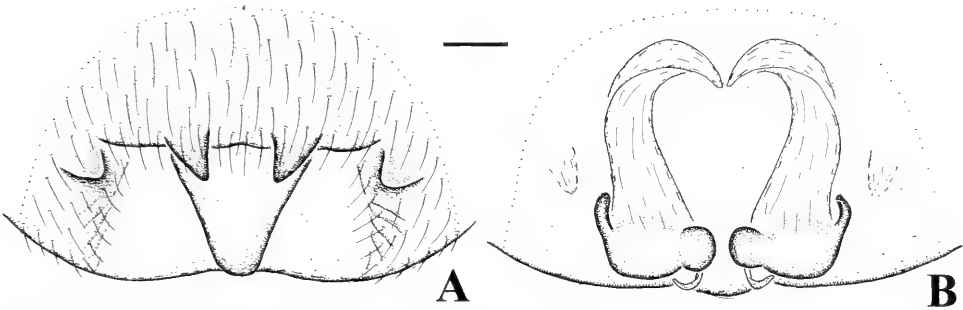


FIGURE 58. *Draconarius schenkeli* (Brignoli). A. Epigynum. B. Vulva.

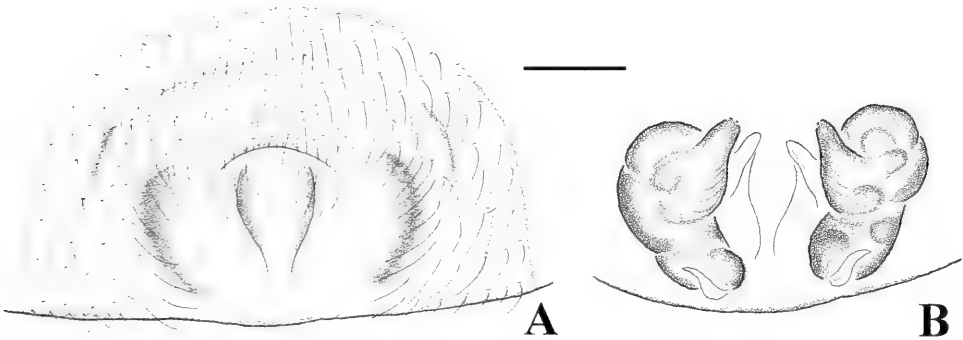


FIGURE 59. *Draconarius simplicidens* Wang, sp. nov. A. Epigynum. B. Vulva.

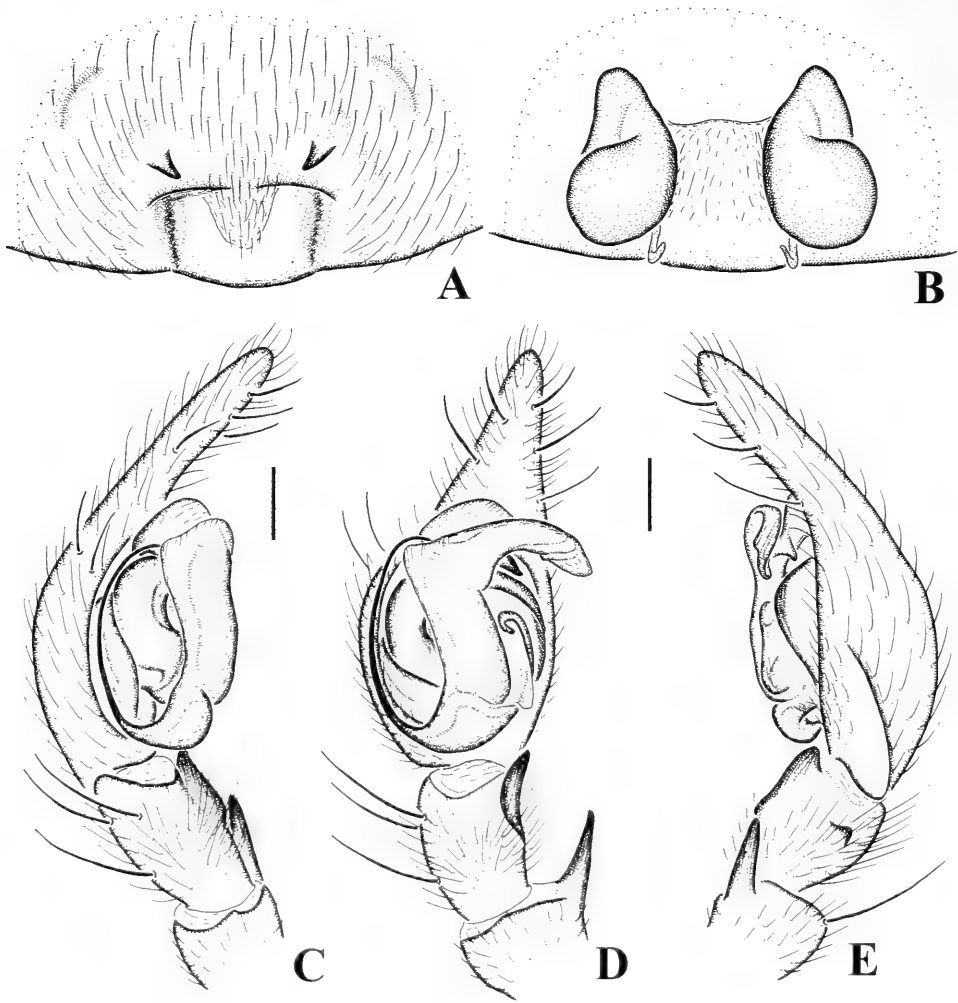


FIGURE 60. *Draconarius singulatus* (Wang et al.). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

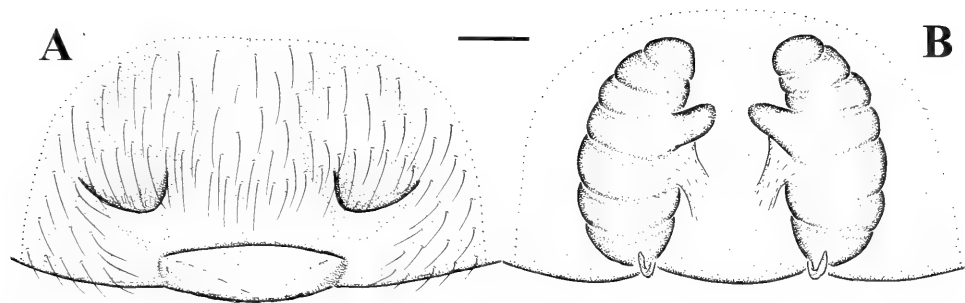


FIGURE 61. *Draconarius stemmleri* (Brignoli). A. Epigynum. B. Vulva.

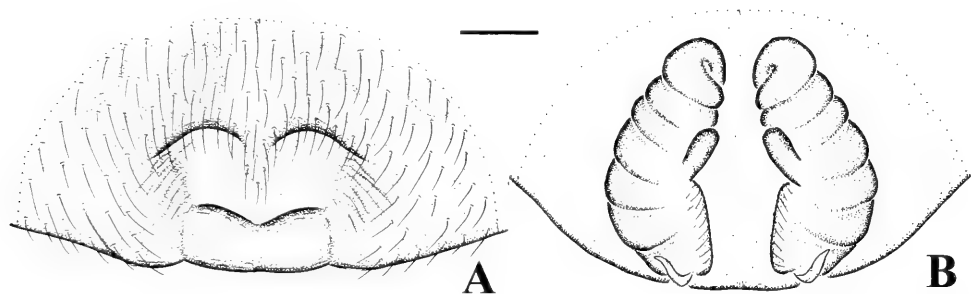


FIGURE 62. *Draconarius striolatus* (Wang et al.). A. Epigynum. B. Vulva.

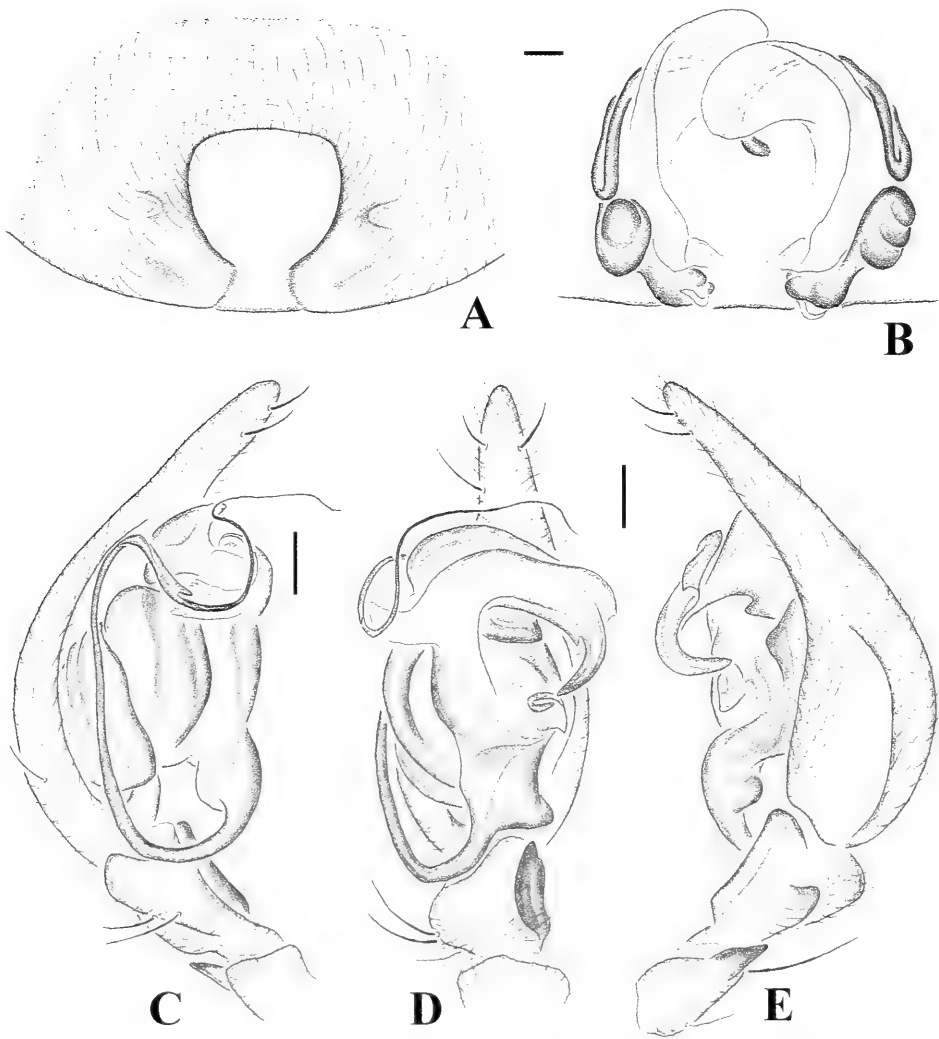


FIGURE 63. *Draconarius terebratus* (Peng and Wang). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.



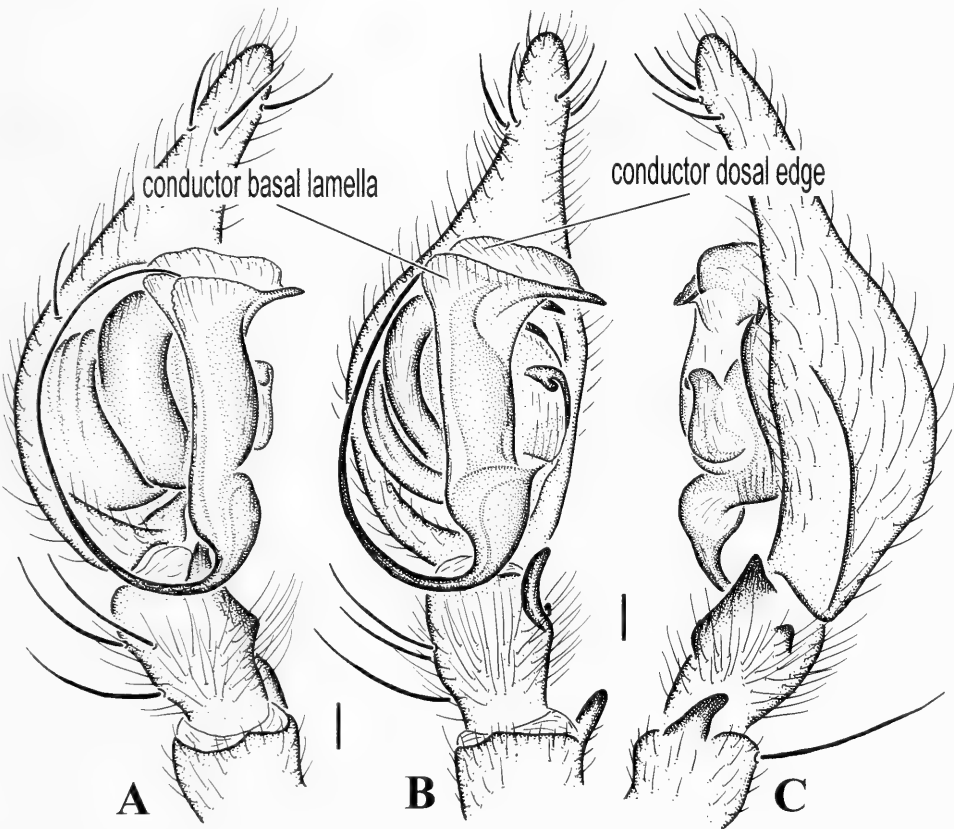


FIGURE 64. *Draconarius tibetensis* Wang, sp. nov. A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

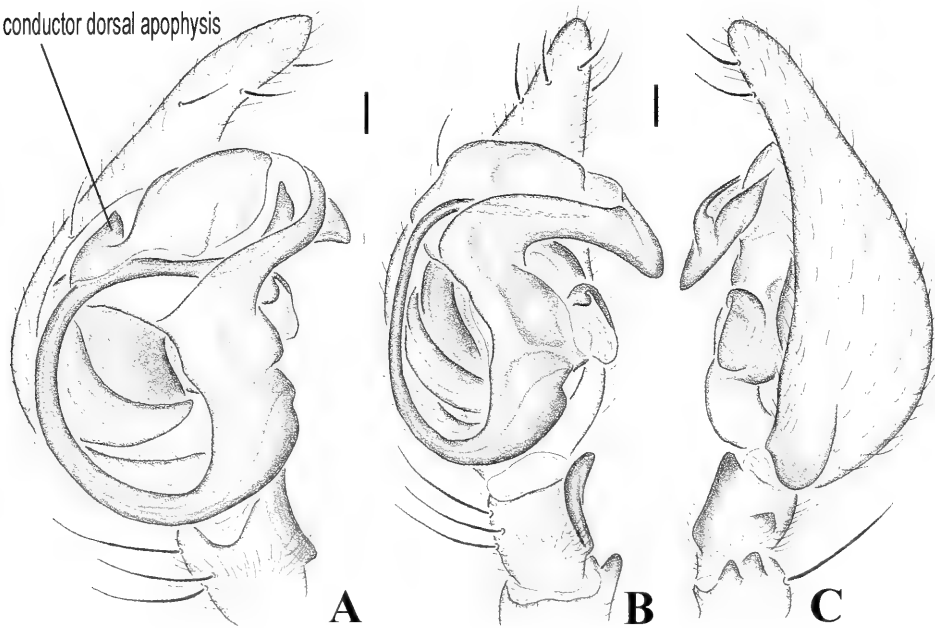


FIGURE 65. *Draconarius uncinatus* (Wang et al.). A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

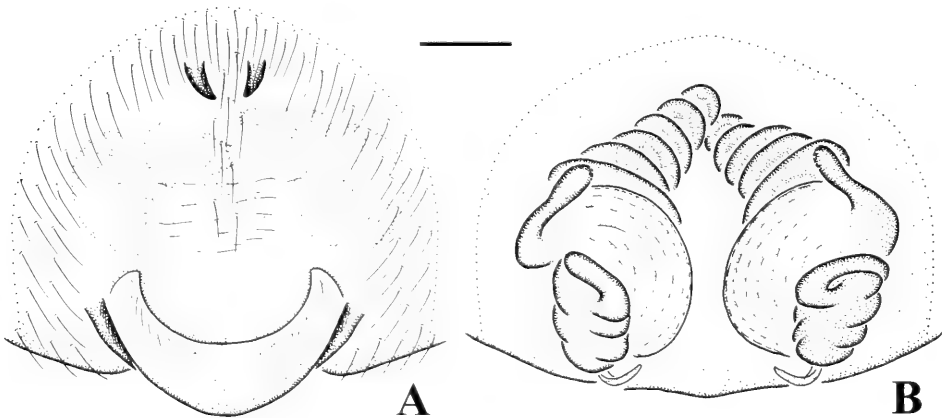


FIGURE 66. *Draconarius wenzhouensis* (Chen). A. Epigynum. B. Vulva.

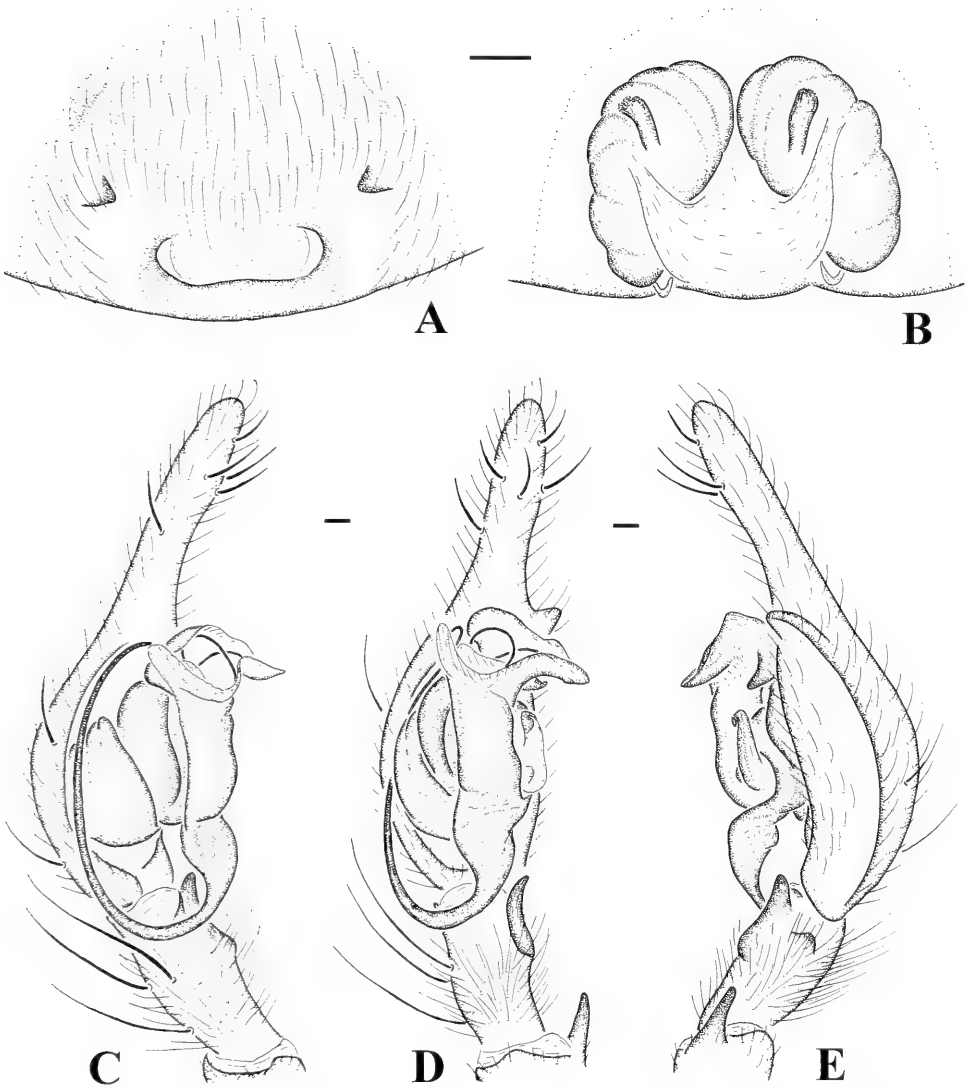


FIGURE 67. *Draconarius wudangensis* (Chen and Zhao). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

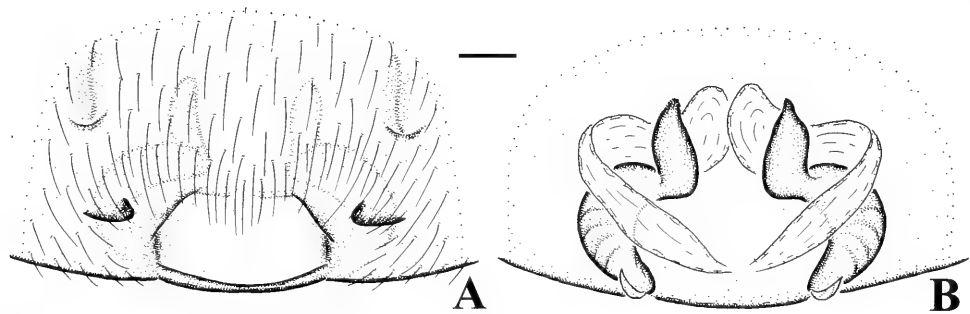


FIGURE 68. *Draconarius wuermlii* (Brignoli). A. Epigynum. B. Vulva.

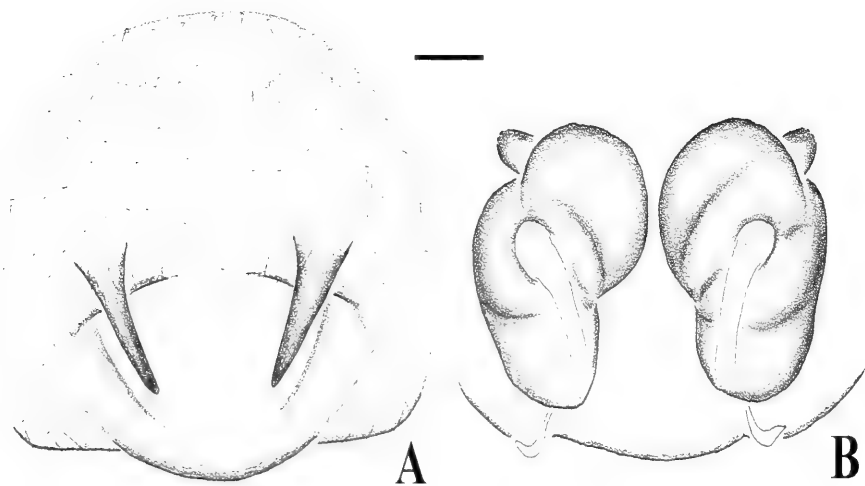


FIGURE 69. *Draconarius yichengensis* Wang, sp. nov. A. Epigynum. B. Vulva.

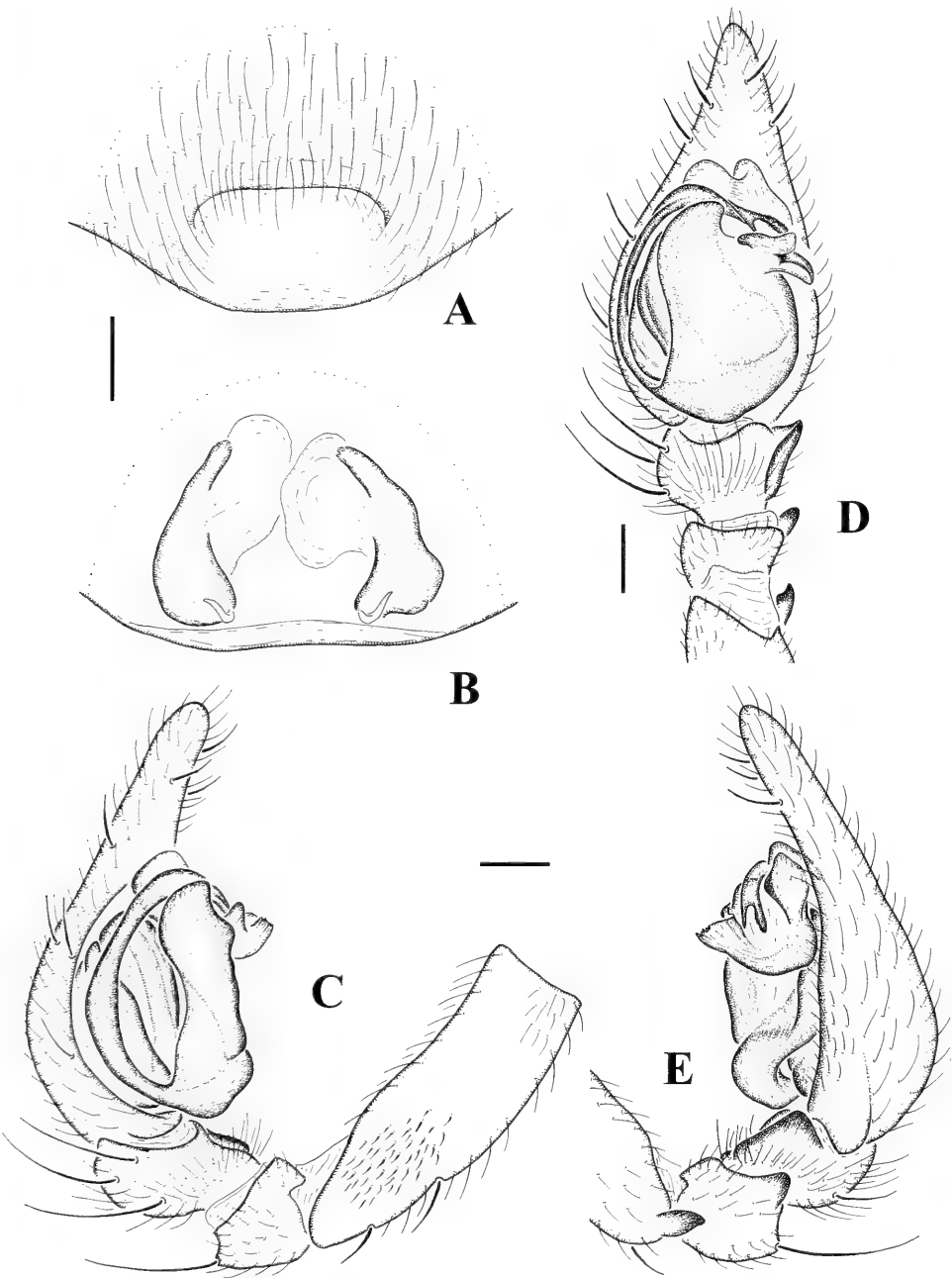


FIGURE 70. *Femoracoelotes latus* (Wang, Tso and Wu). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

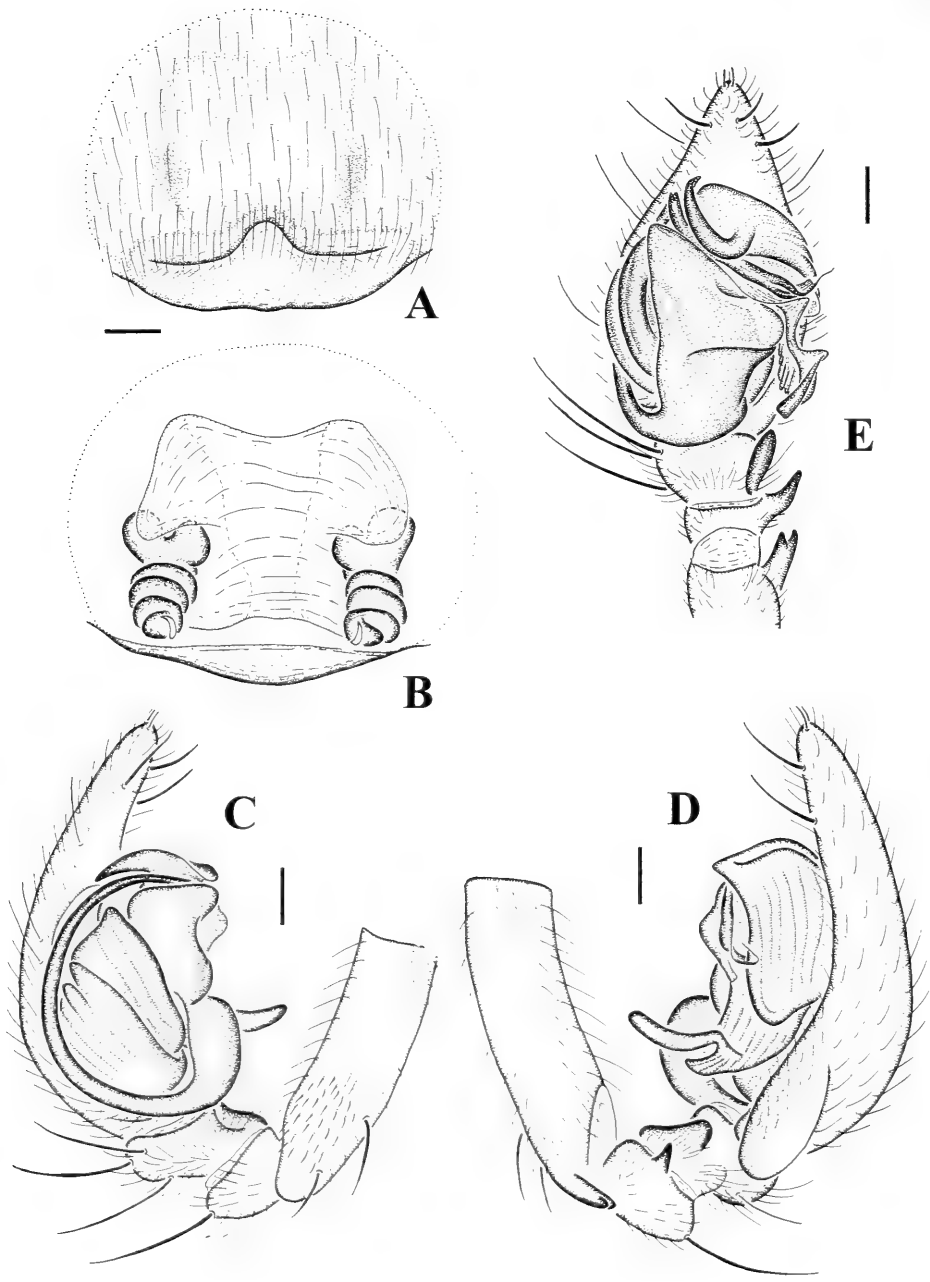


FIGURE 71. *Femoracoelotes plamicki* (Wang and Ono). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, retrolateral view. E. Pedipalpus, ventral view.

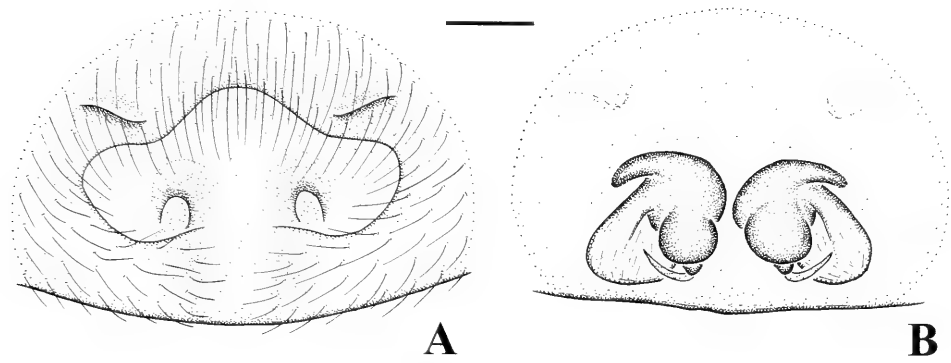


FIGURE 72. *Leptocoelotes edentulus* (Wang and Ono). A. Epigynum. B. Vulva.

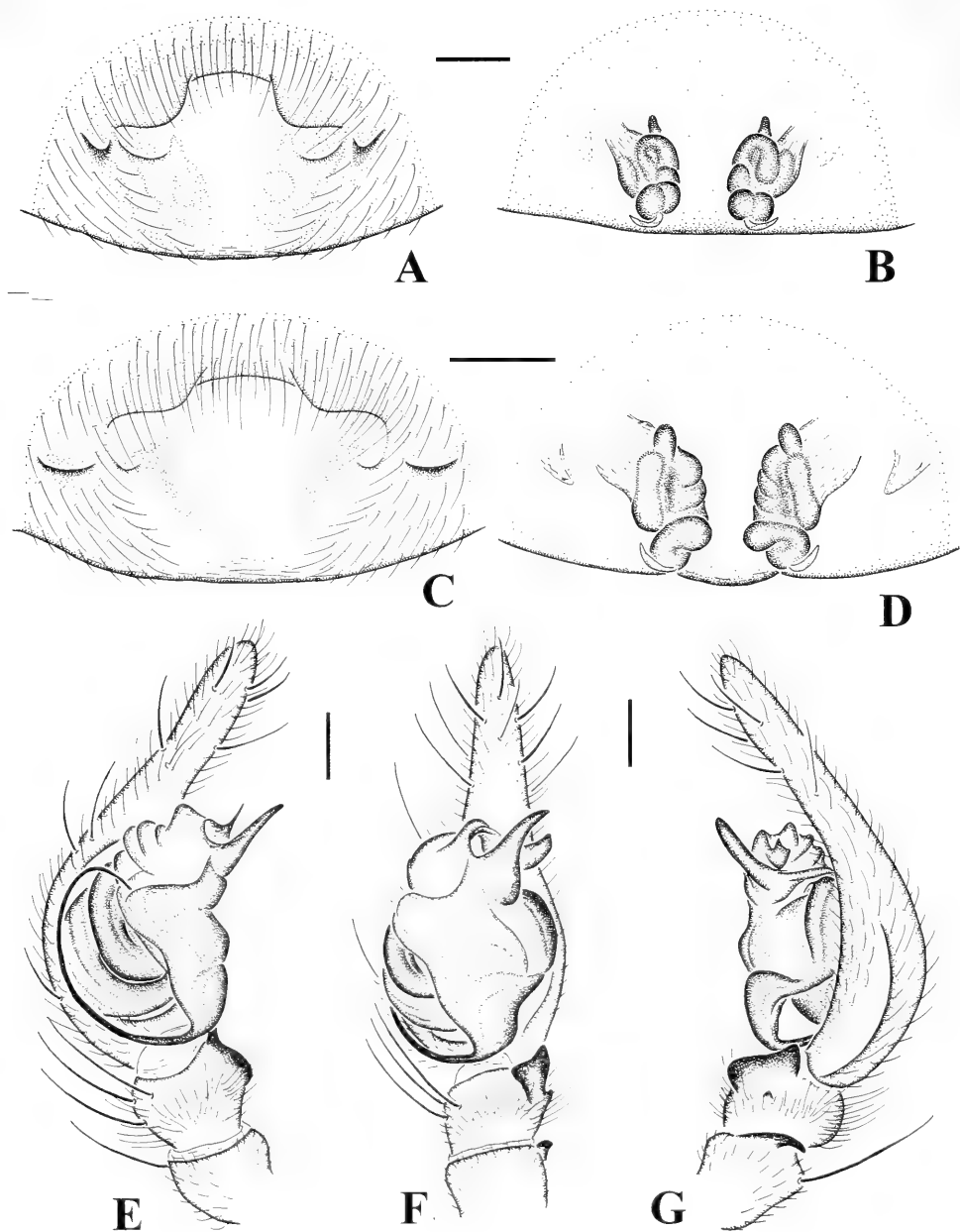


FIGURE 73. *Leptocoelotes pseudolunifomis* (Zhang, Peng and Kim). A, C. Epigyna, showing variation. B, D. Vulvae, showing variation. E. Pedipalpus, prolateral view. F. Pedipalpus, ventral view. G. Pedipalpus, retrolateral view.



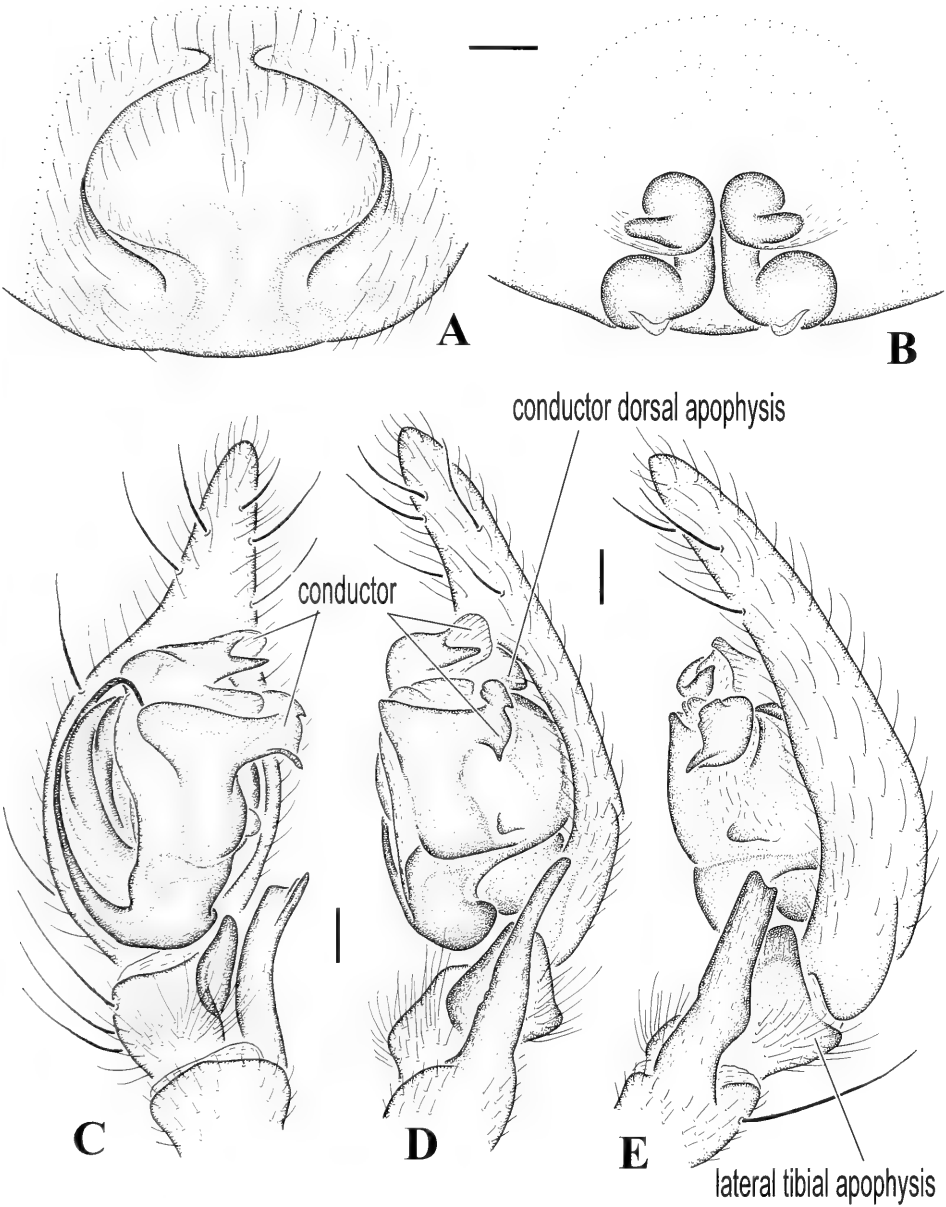


FIGURE 74. *Longicoelotes karschi* Wang. A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

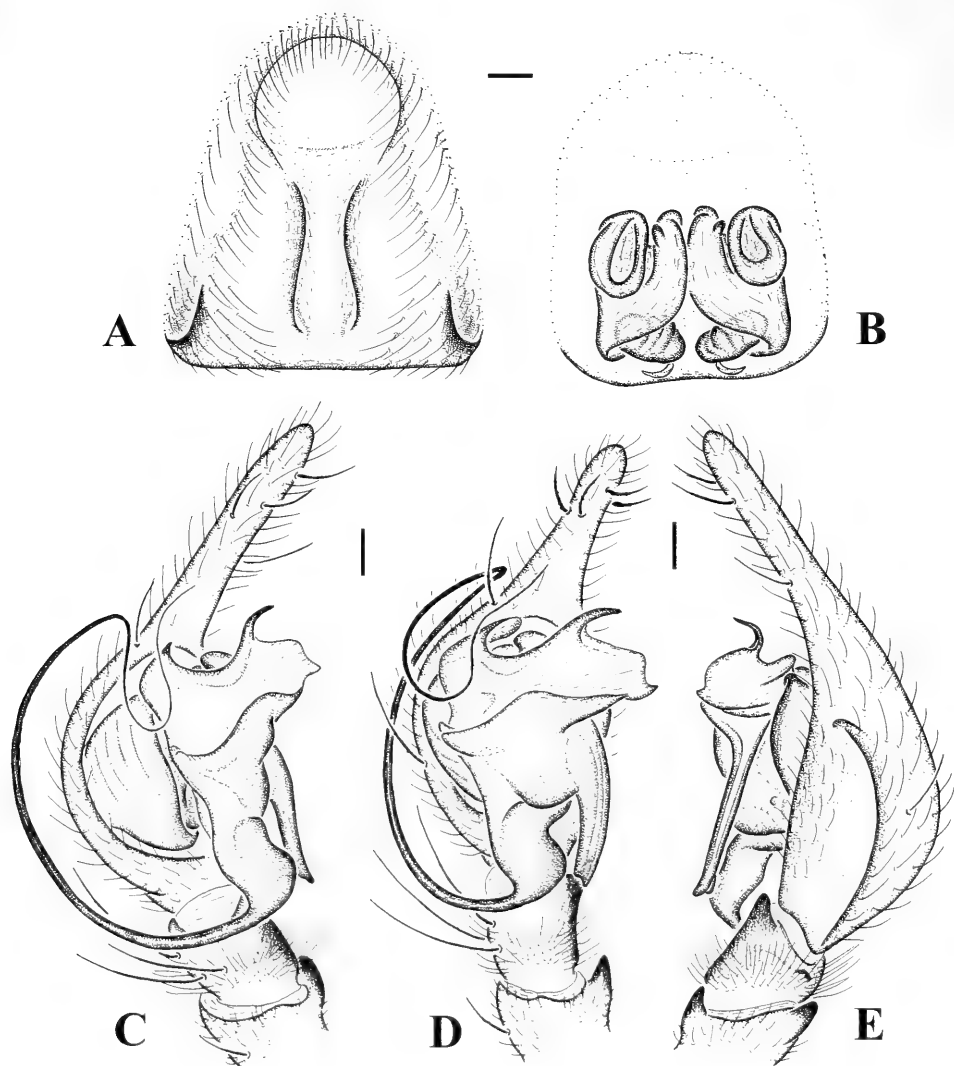


FIGURE 75. *Platocoelotes impletus* (Peng and Wang). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

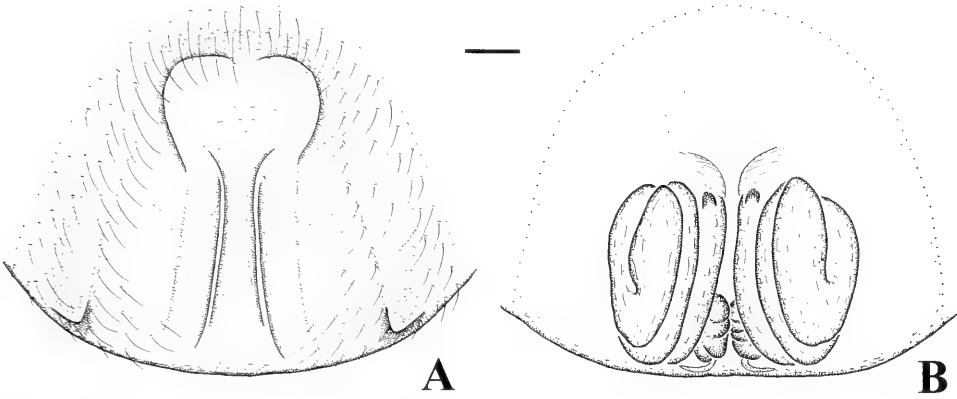


FIGURE 76. *Platocoelotes icohamatoides* (Peng and Wang). A. Epigynum. B. Vulva.

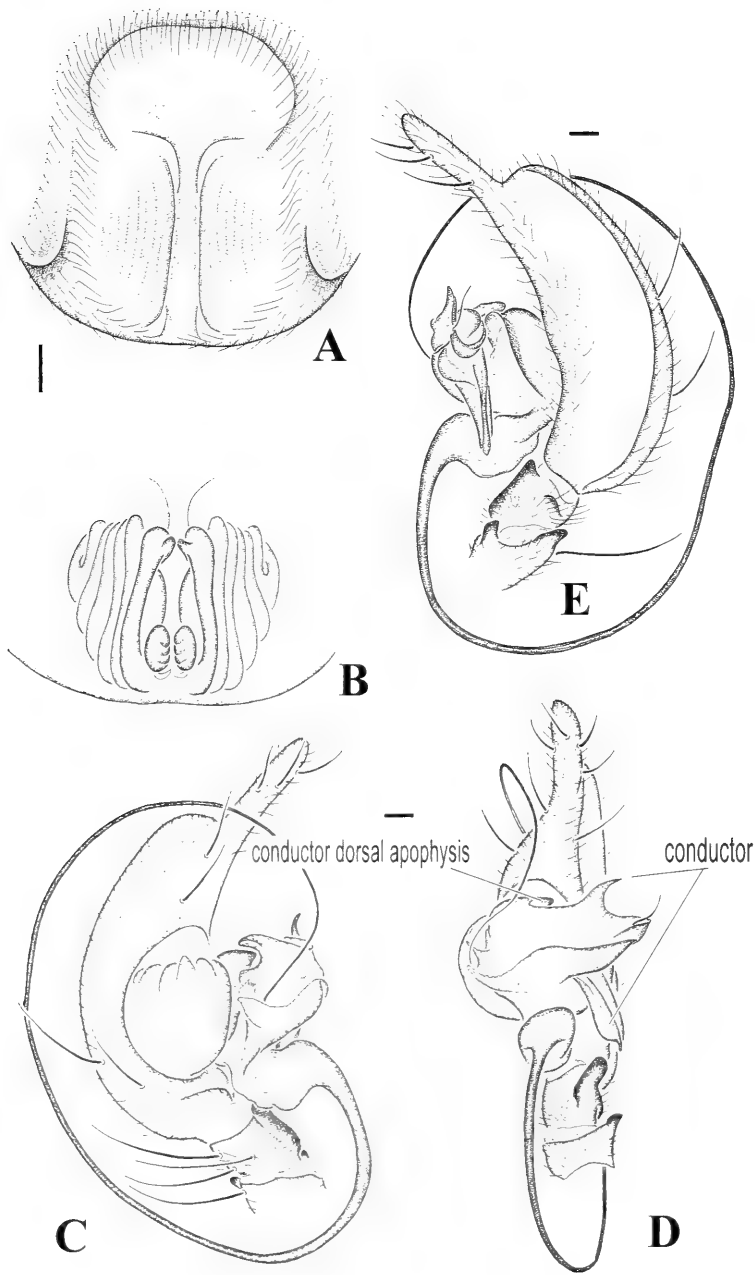


FIGURE 77. *Platocoelotes kailiensis* Wang, sp. nov. A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

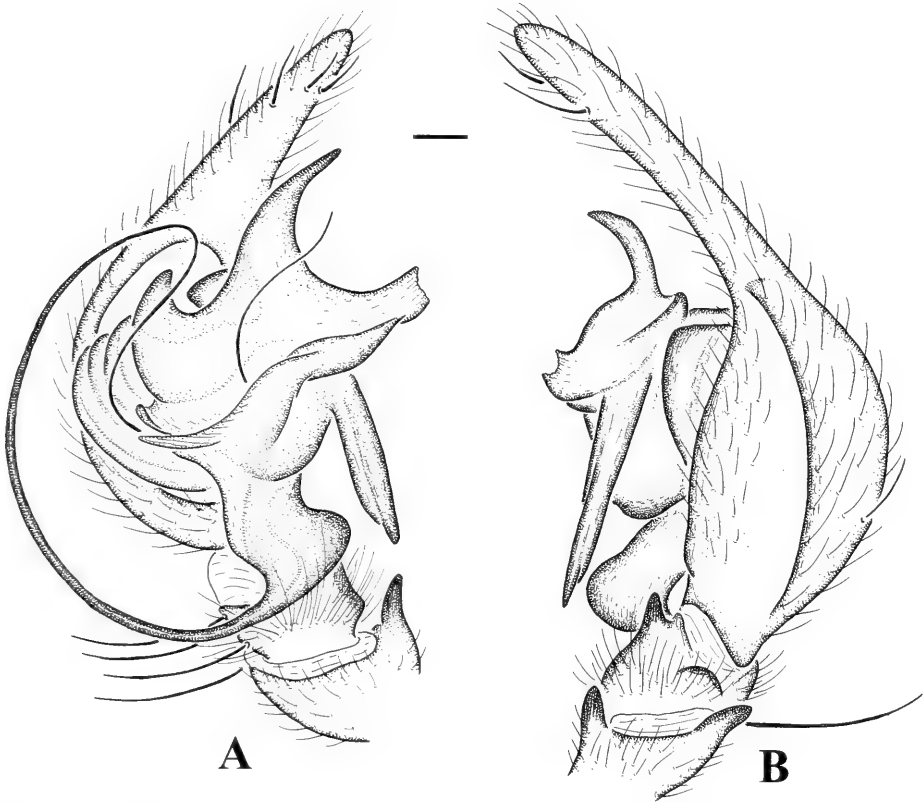


FIGURE 78. *Platocoelotes lichuanensis* (Chen and Zhao). A. Pedipalpus, prolateral view. B. Pedipalpus, retrolateral view.

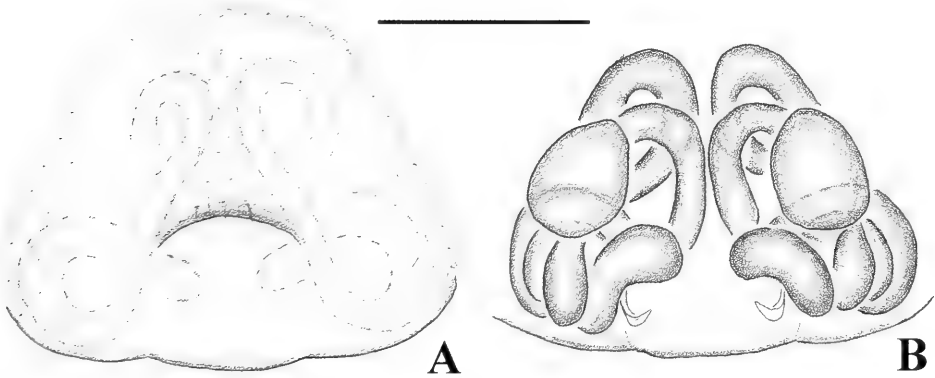


FIGURE 79. *Spiricoelotes pseudozonatus* Wang, sp. nov. A. Epigynum. B. Vulva.

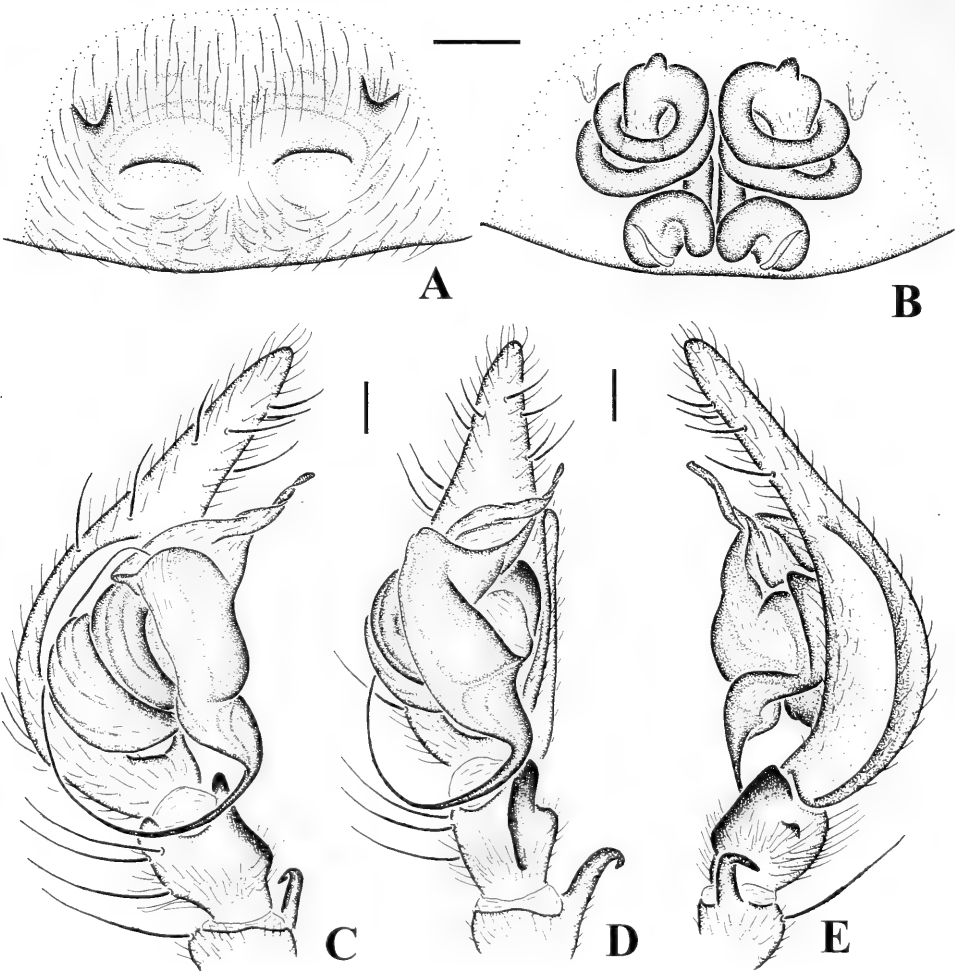


FIGURE 80. *Spiricoelotes zonatus* (Peng and Wang). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

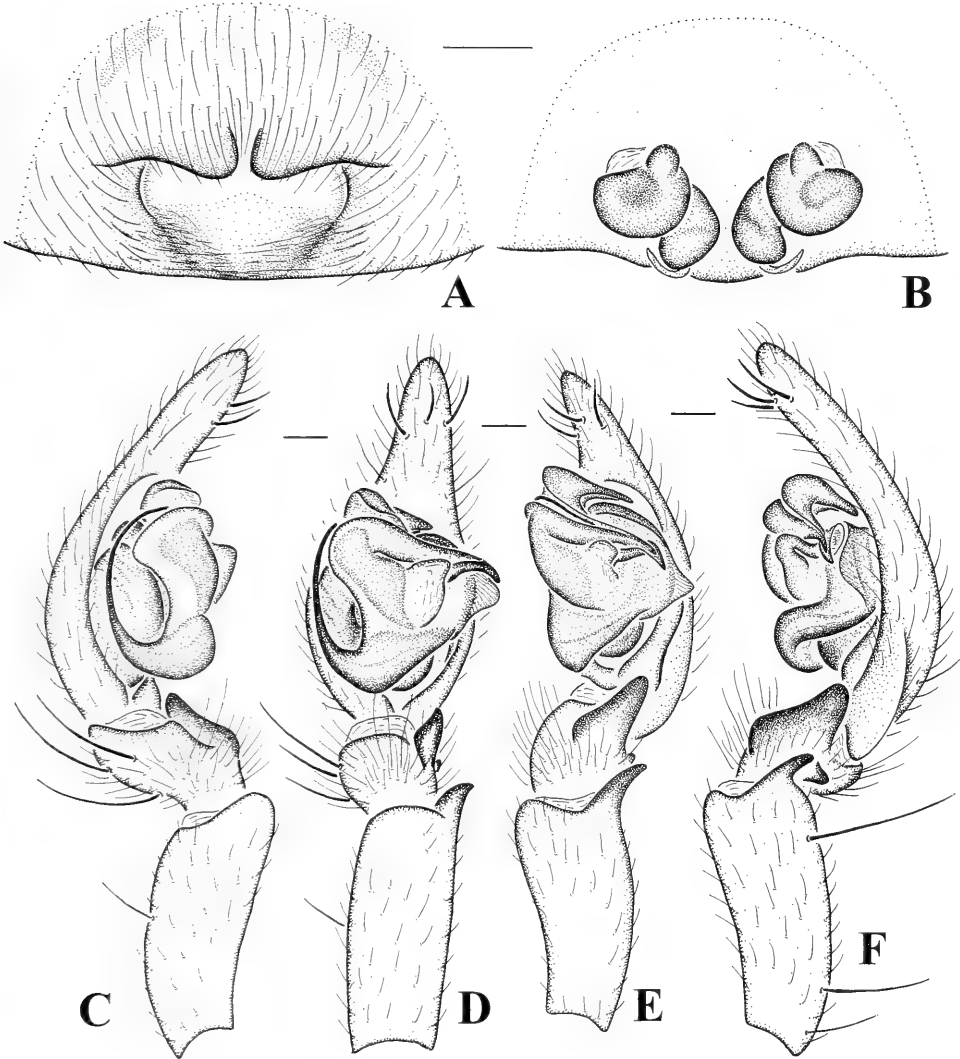


FIGURE 81. *Tegocoelotes secundus* (Paik). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E, F. Pedipalpus, retrolateral view.

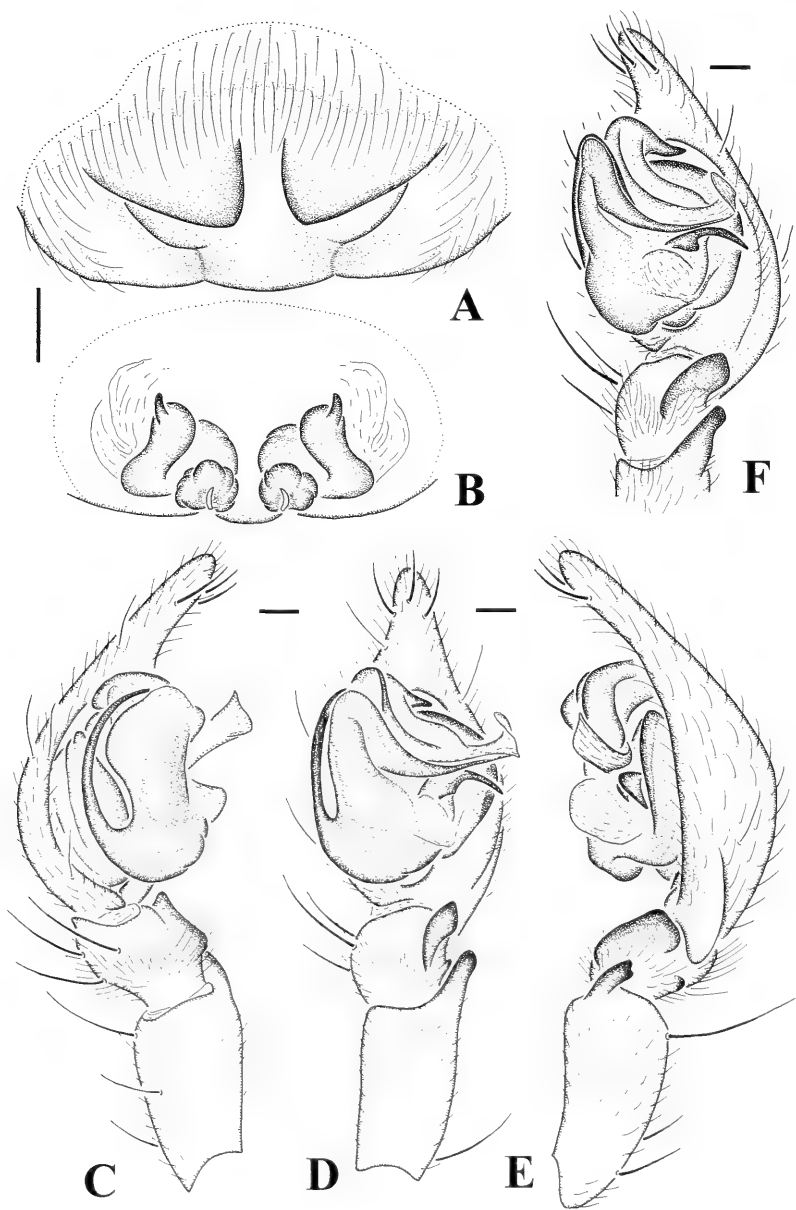


FIGURE 82. *Tegocoelotes corasides* (Bösenberg and Strand). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. F. Pedipalpus, retrolateral view.



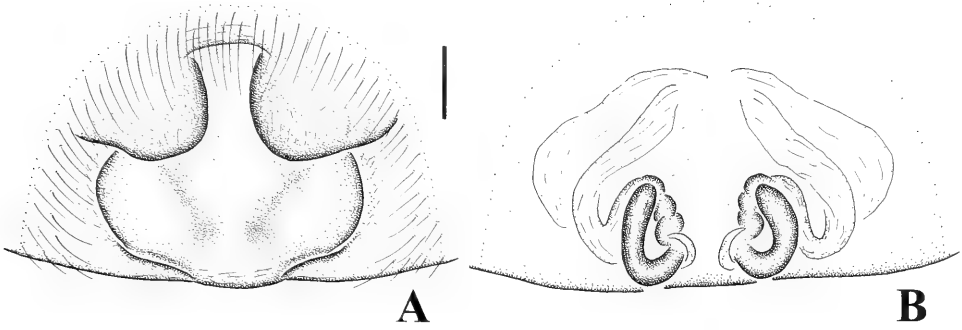


FIGURE 83. *Tegecoelotes ignotus* (Bösenberg and Strand). A. Epigynum. B. Vulva.

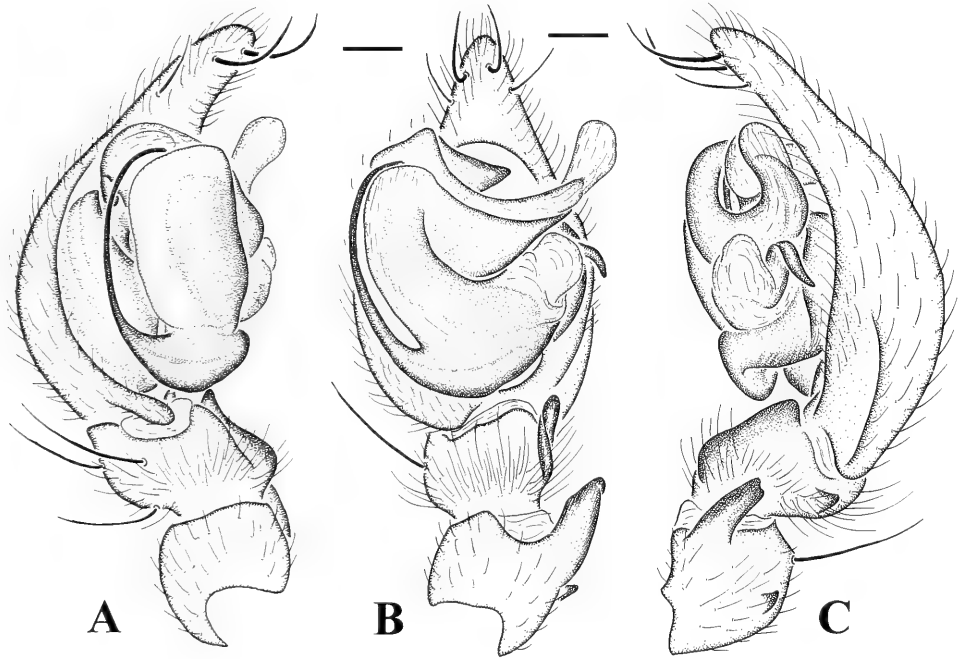


FIGURE 84. *Tegecoelotes muscicapus* (Bösenberg and Strand). A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.

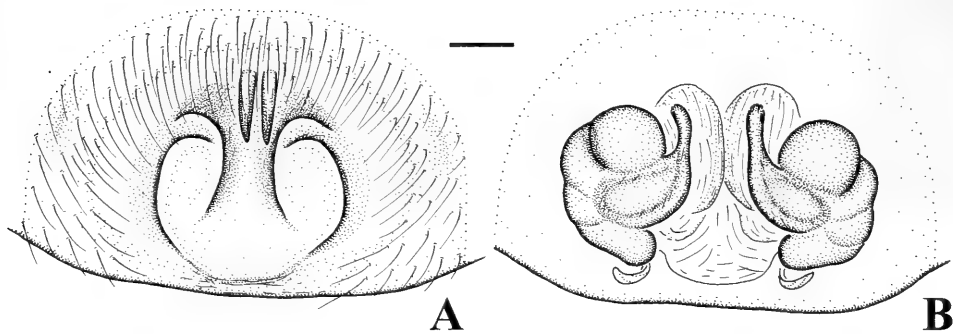


FIGURE 85. *Tonsilla eburniformis* Wang and Yin. A. Epigynum. B. Vulva.

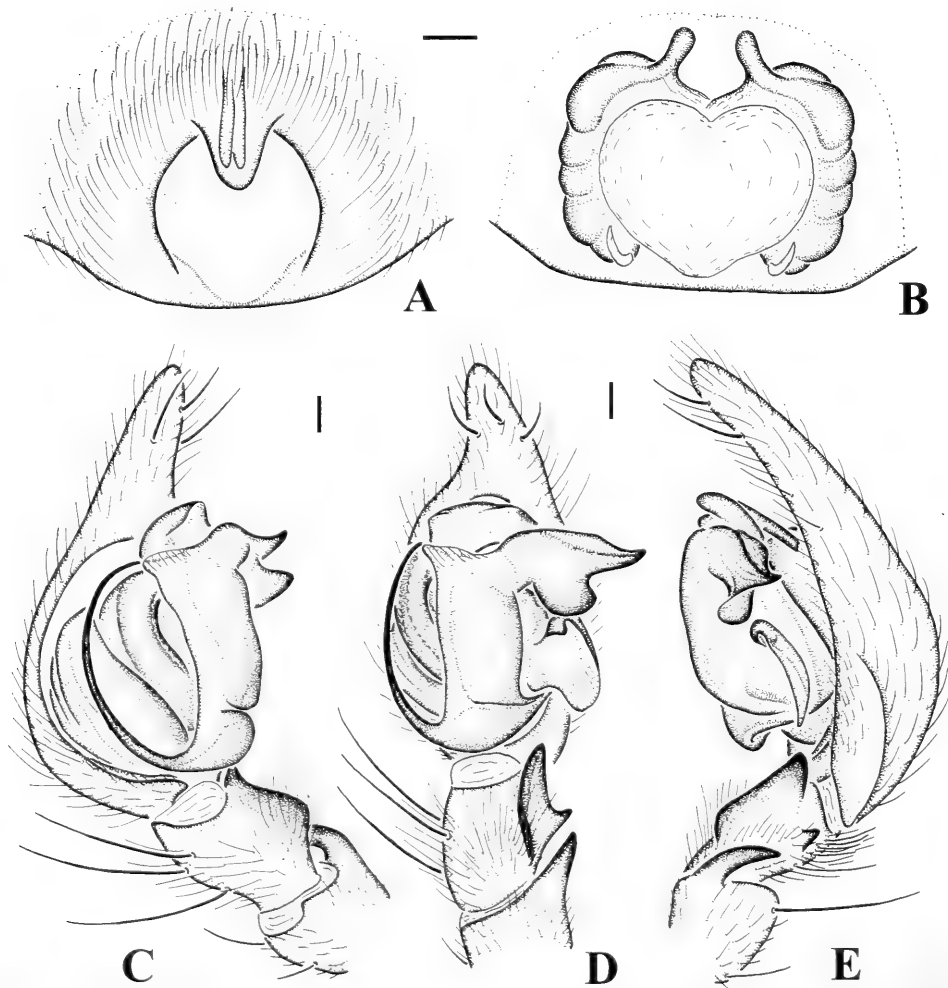


FIGURE 86. *Tonsilla truculenta* Wang and Yin, female holotype, male allotype, from Tianzishan, Sangzhi, Hunan, China. A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E. Pedipalpus, retrolateral view.

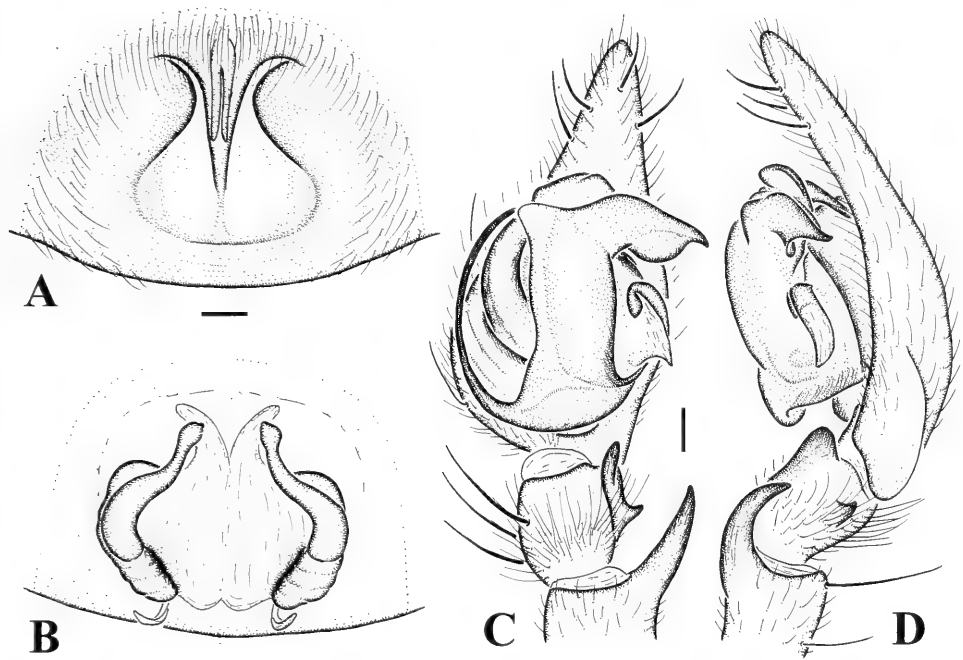


FIGURE 87. *Tonsilla truculenta* Wang and Yin, variation one, male and female paratypes from Tianzishan, Sangzhi, Hunan, China, the same locality as holotype female. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D. Pedipalpus, retrolateral view.

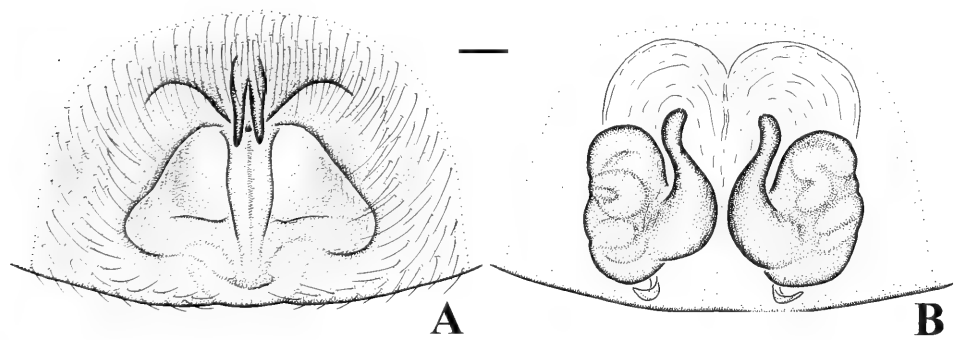


FIGURE 88. *Tonsilla truculenta* Wang and Yin, variation two, female paratype from Tianzishan, Sangzhi, Hunan, China, the same locality as holotype female. A. Epigynum. B. Vulva.

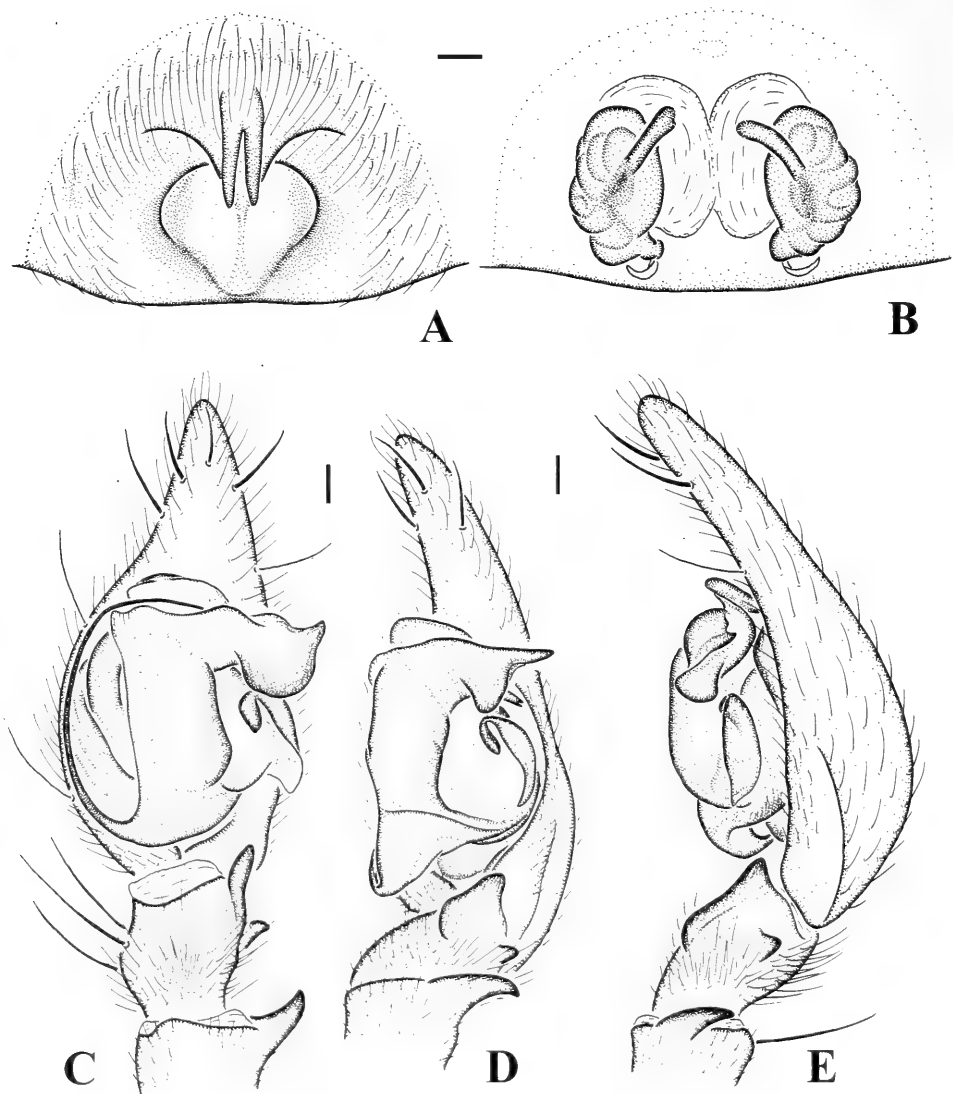


FIGURE 89. *Tonsilla truculenta* Wang and Yin, variation three, females and male from Guiyang, Guizhou, China. A. Epigynum. B. Vulva. C. Pedipalpus, ventral view. D, E. Pedipalpi, retrolateral view.

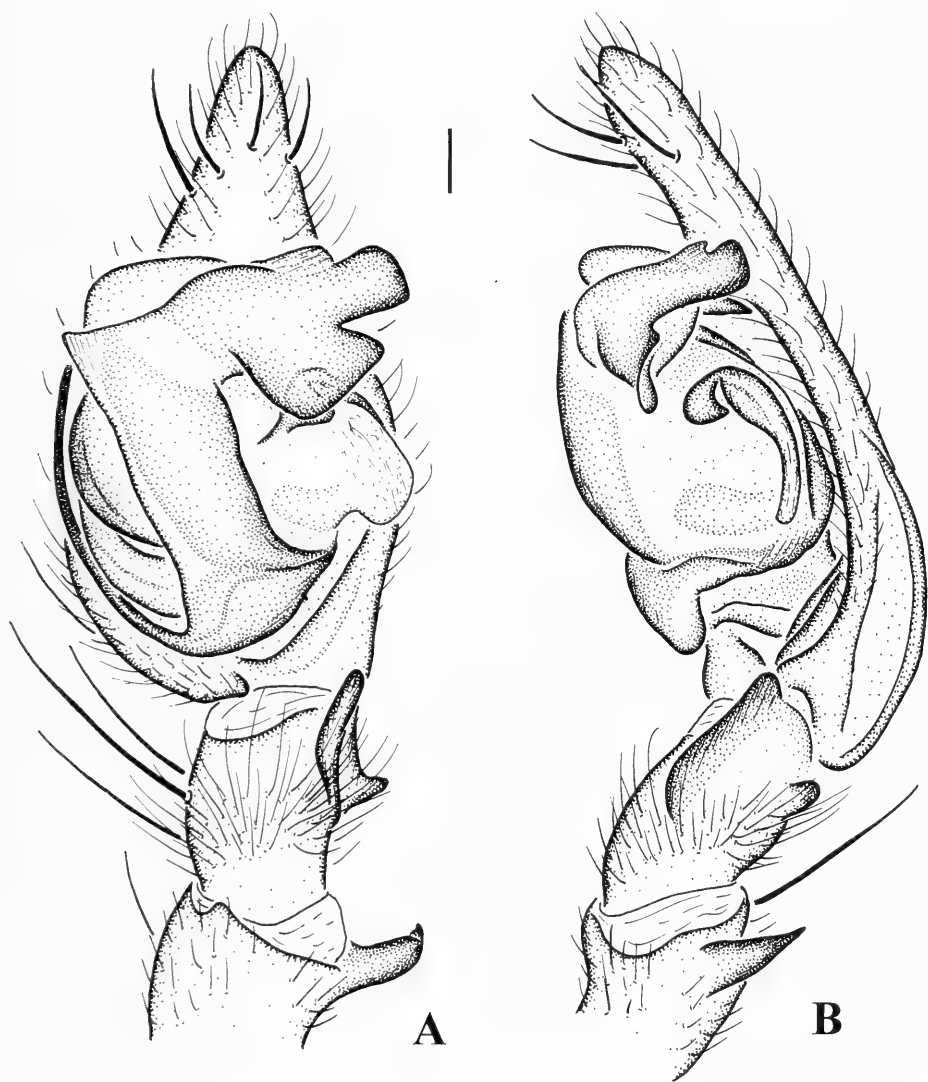


FIGURE 90. *Tonsilla truculenta* Wang and Yin, variation four, male from Guiyang, Guizhou, China. A. Pedipalpus, ventral view. B. Pedipalpus, retrolateral view.

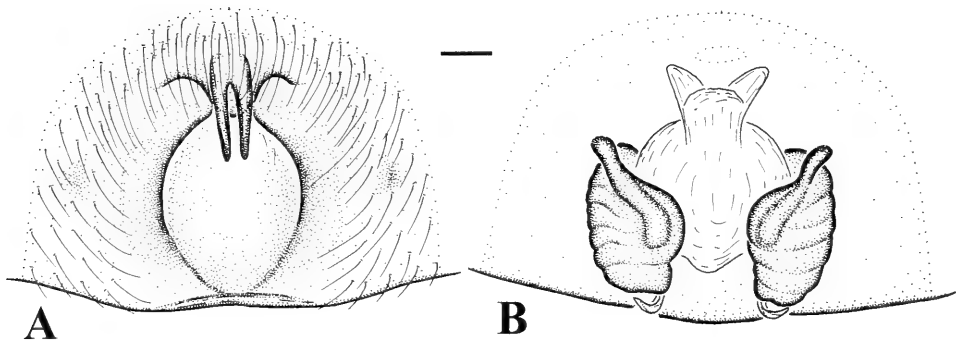


FIGURE 91. *Tonsilla truculenta* Wang and Yin, variation five, female paratype from Meitan, Guizhou, China. A. Epigynum. B. Vulva.

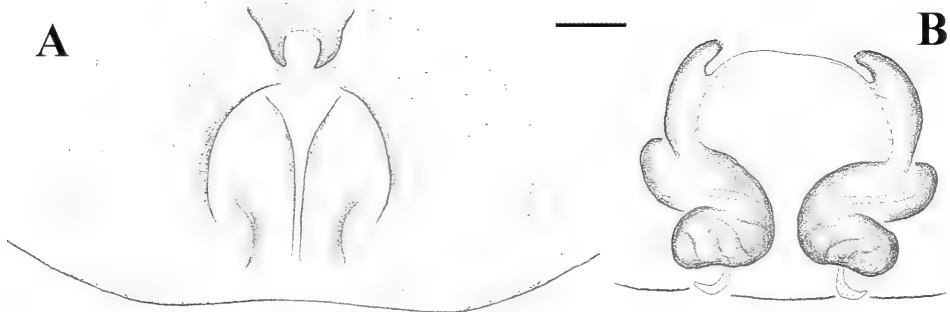


FIGURE 92. *Tonsilla lyratus* (Wang et al.). A. Epigynum. B. Vulva.

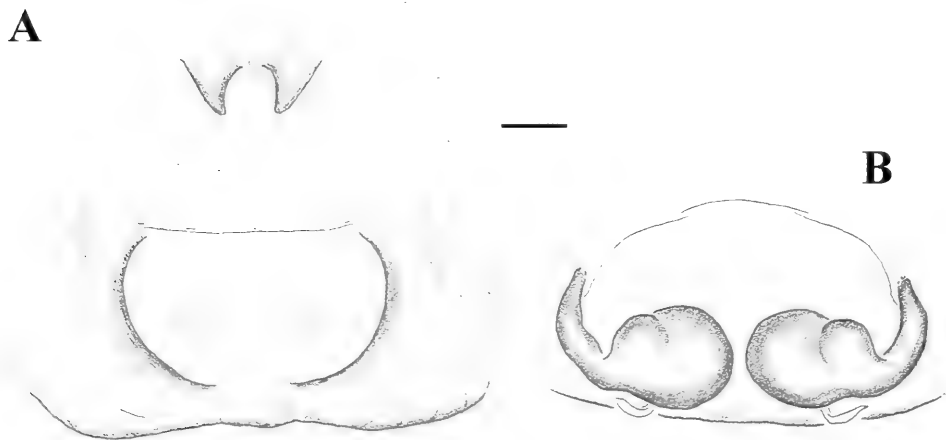


FIGURE 93. *Tonsilla tautispinus* (Wang et al.). A. Epigynum. B. Vulva.

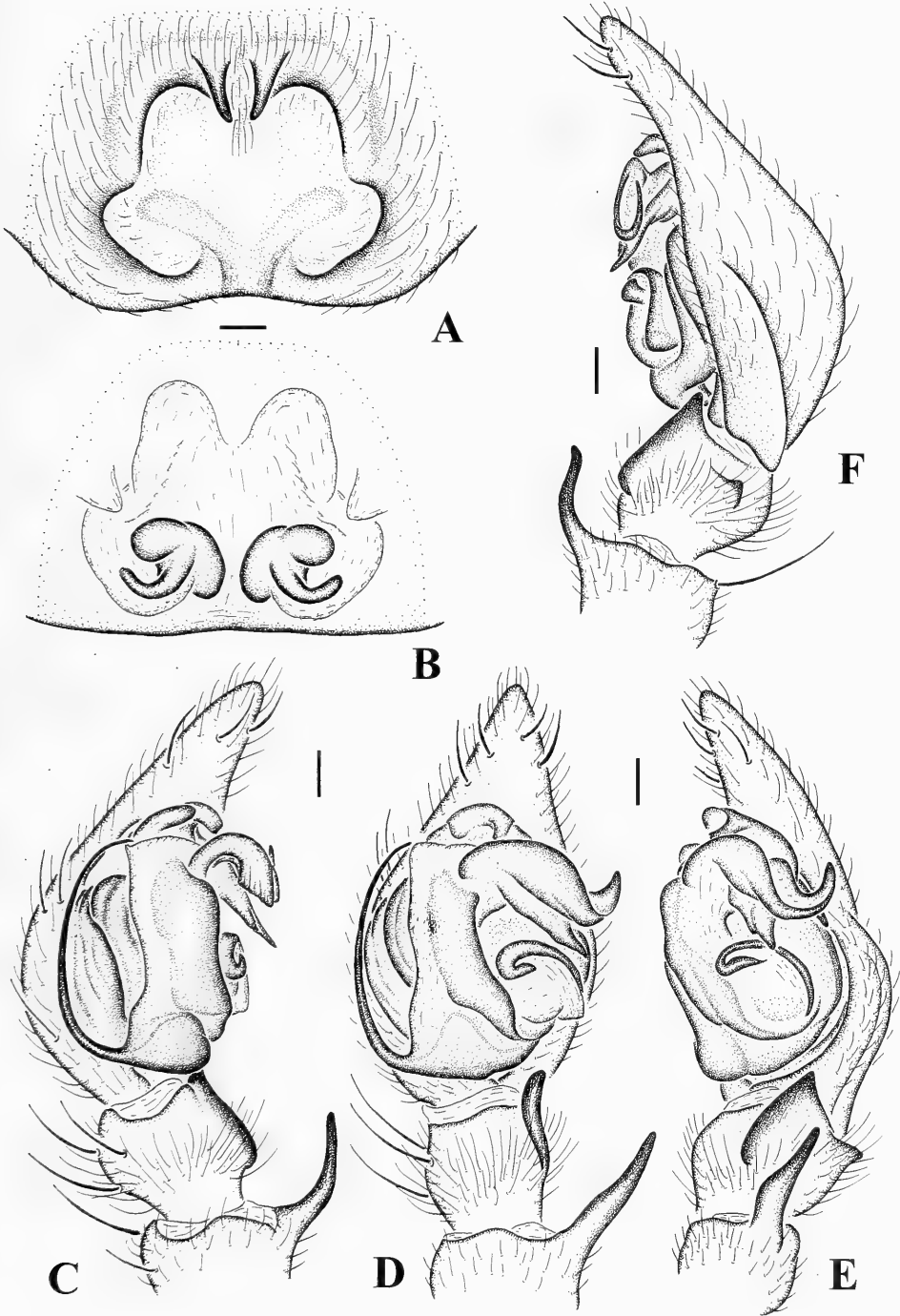


FIGURE 94. *Tonsilla variegatus* (Wang et al.). A. Epigynum. B. Vulva. C. Pedipalpus, prolateral view. D. Pedipalpus, ventral view. E, F. Pedipalpi, retrolateral view.

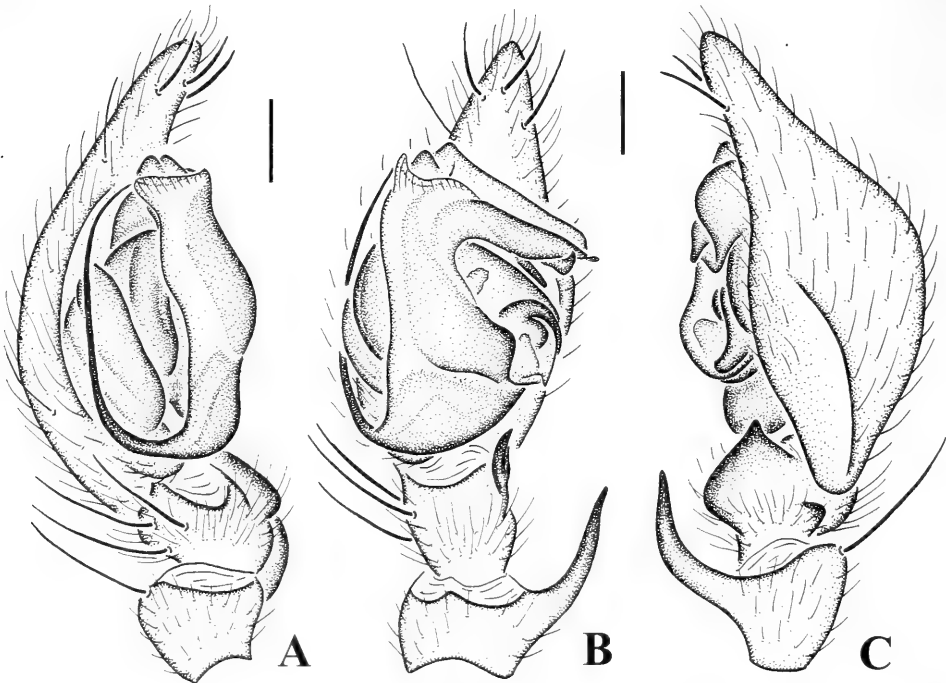


FIGURE 95. *Tonsilla makros* Wang, sp. nov. A. Pedipalpus, prolateral view. B. Pedipalpus, ventral view. C. Pedipalpus, retrolateral view.



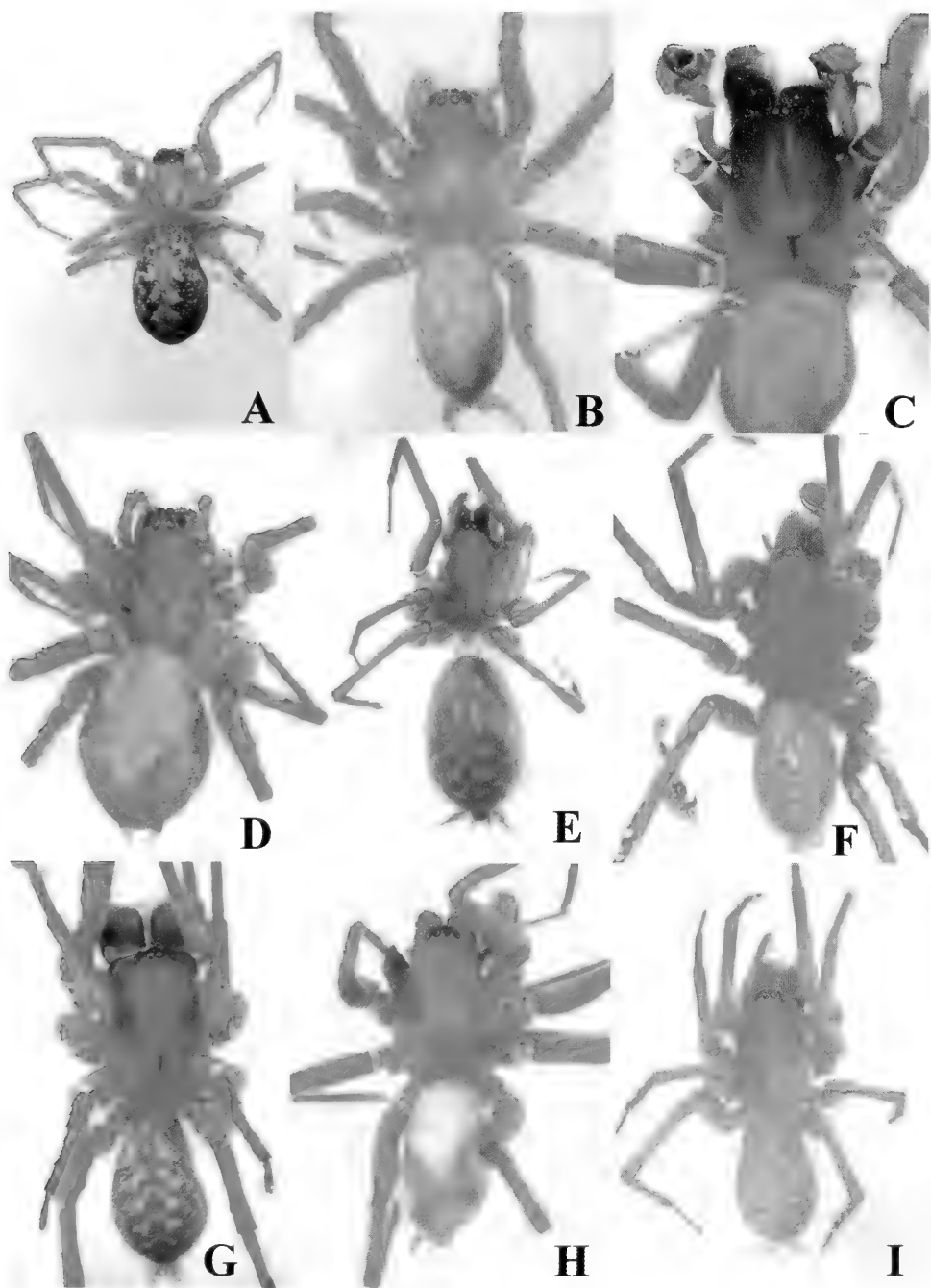
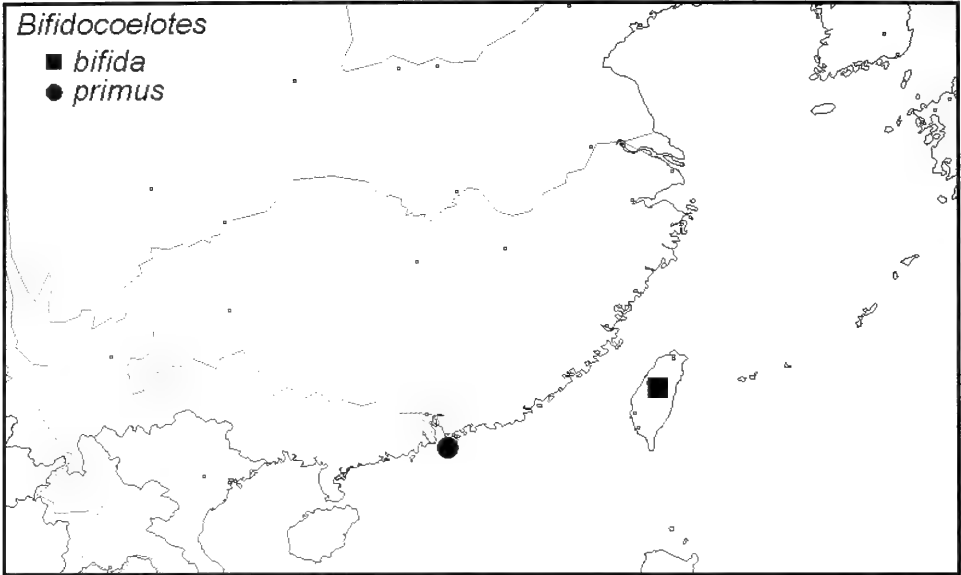


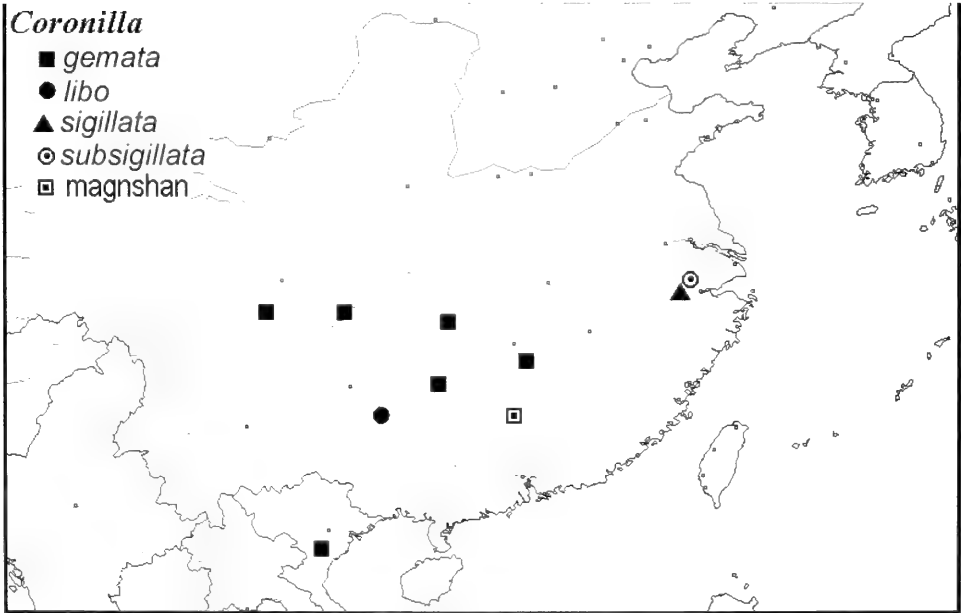
FIGURE 96. Habitus of *Draconarius*, dorsal views. A. *Draconarius haopingensis*, female. B. *Draconarius jiangyongensis*, female. C. *Draconarius ornatus*, male. D. *Draconarius molluscus*, female. E. *Draconarius parabruneus*, female. F. *Draconarius uncinatus*, male. G. *Draconarius terebratus*, female. H. *Draconarius terebratus*, male. I. *Draconarius rufulus*, female.



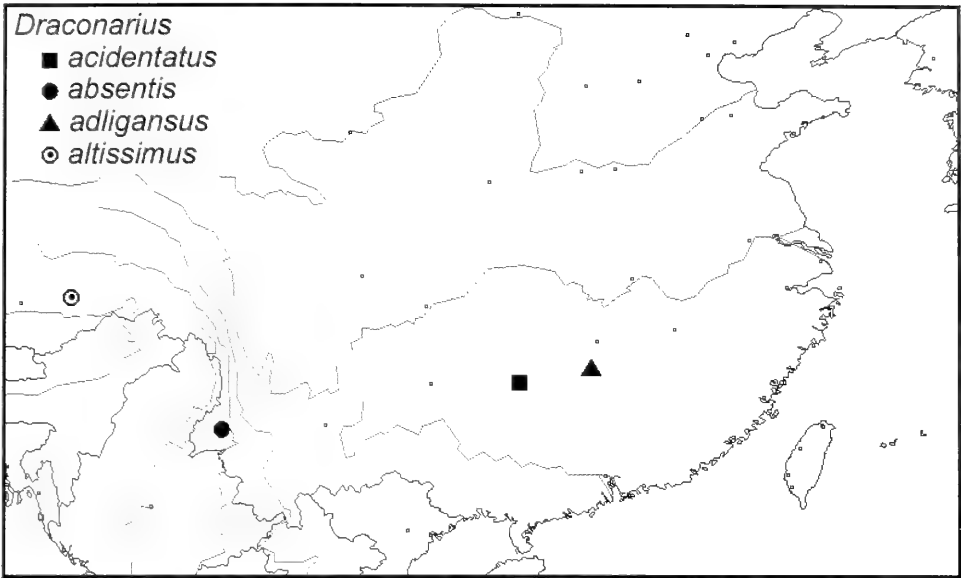
FIGURE 97. Habitus of *Coelotinae*, dorsal views. A. *Draconarius acidentatus*, female. B. *Draconarius adligansus*, female. C. *Draconarius baxiantaiensis*, female. D. *Draconarius calcariformis*, female. E. *Draconarius chaigiaoensis*, female. F. *Draconarius shuangpaiensis* (= *Draconarius digitusiformis*), male. G. *Bifidocoelotes primus*, female. H. *Tonsilla lyratus*, female. I. *Spiricoelotes zonatus*, female.



MAP 1. East Asia, showing distribution of *Bifidocoelotes* species.



MAP 2. East Asia, showing distribution of *Coronilla* species.



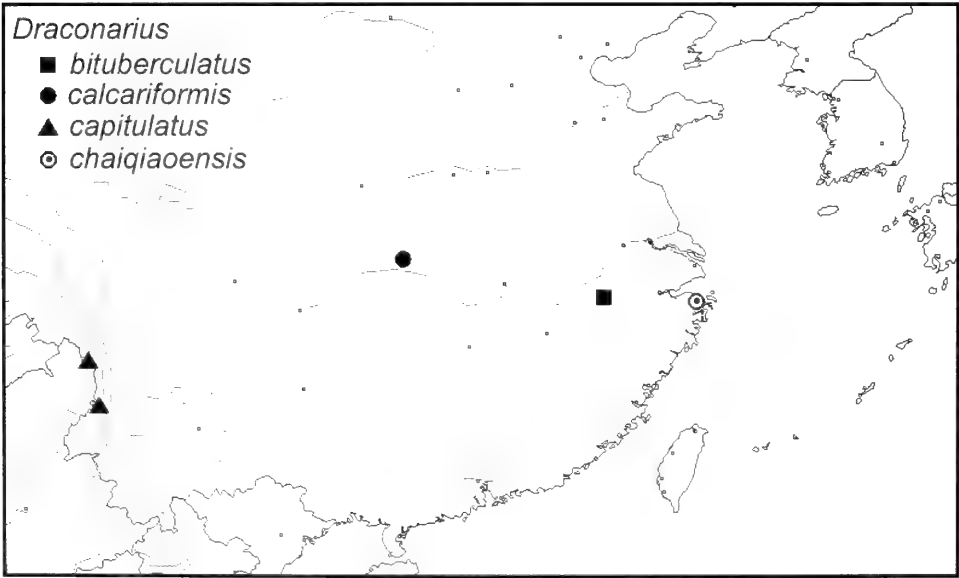
MAP 3. East Asia, showing distribution of *Draconarius absentis*, *D. acidentatus*, *D. adligansus*, and *D. altissimus*.



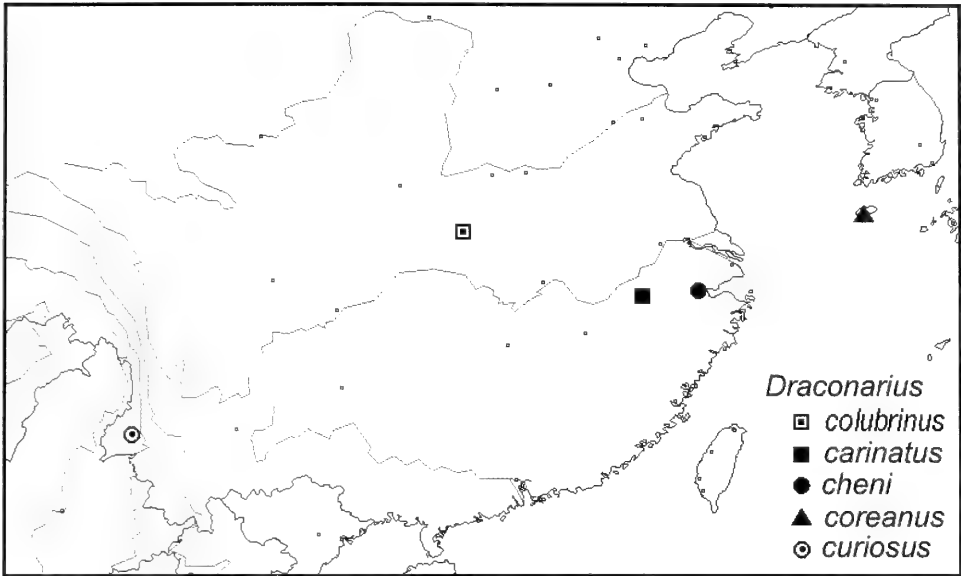
MAP 4. East Asia, showing distribution of *Draconarius agrestis*, *D. amygdaliformis*, *D. arcuatus*, and *D. argenteus*.



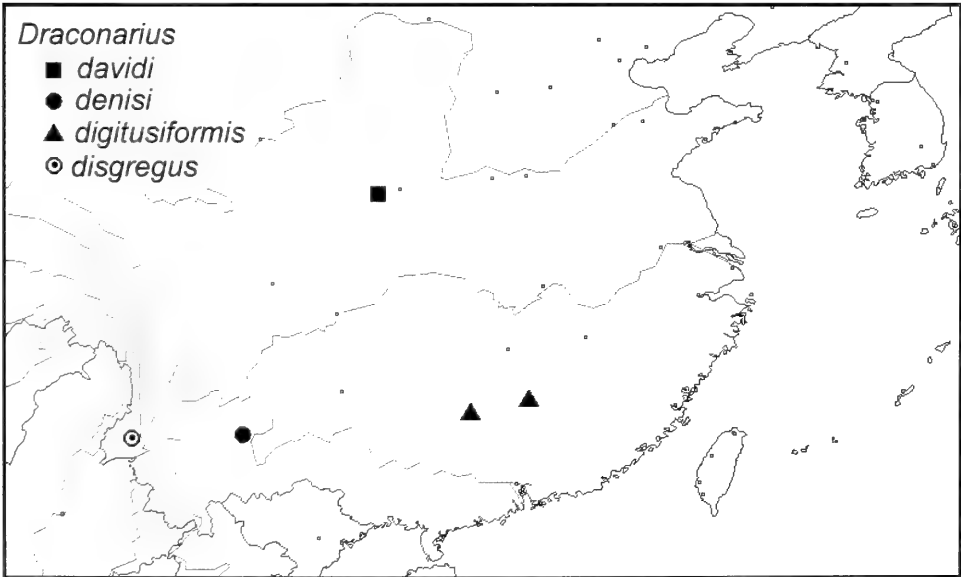
MAP 5. East Asia, showing distribution of *Draconarius aspinatus*, *D. baronii*, *D. baxiantaiensis*, and *D. brunneus*.



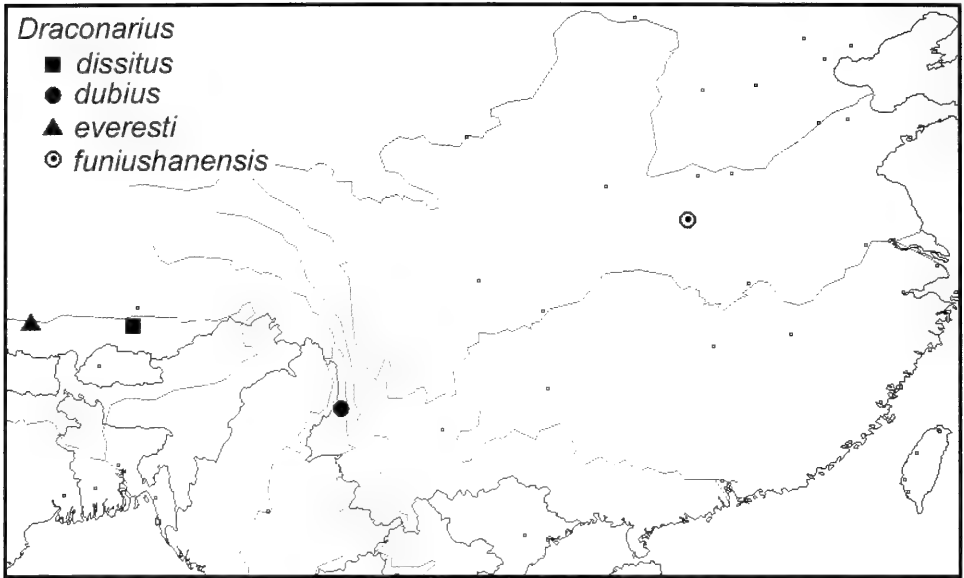
MAP 6. East Asia, showing distribution of *Draconarius bituberculatus*, *D. calcariformis*, *D. capitulatus*, and *D. chaiqiaoensis*.



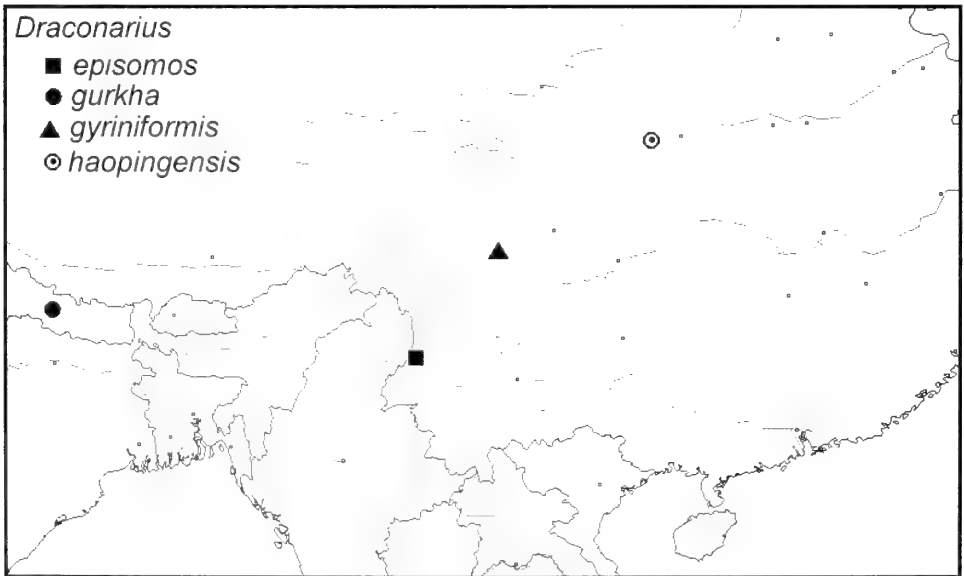
MAP 7. East Asia, showing distribution of *Draconarius carinatus*, *D. cheni*, *D. coreanus*, and *D. curiosus*.



MAP 8. East Asia, showing distribution of *Draconarius davidi*, *D. denisi*, *D. digitusiformis*, and *D. disgregus*.

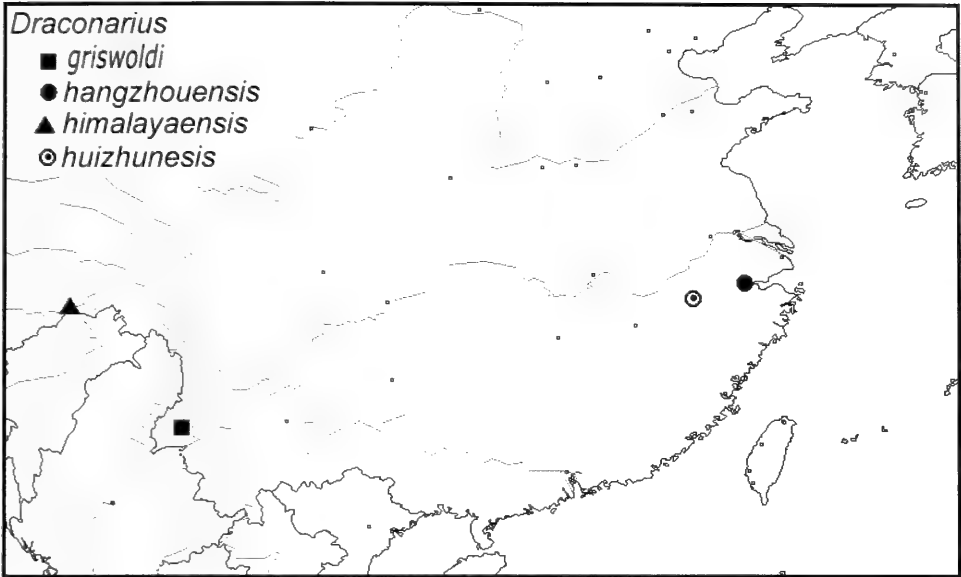


MAP 9. East Asia, showing distribution of *Draconarius dissitus*, *D. dubius*, *D. everesti*, and *D. funiushanensis*.

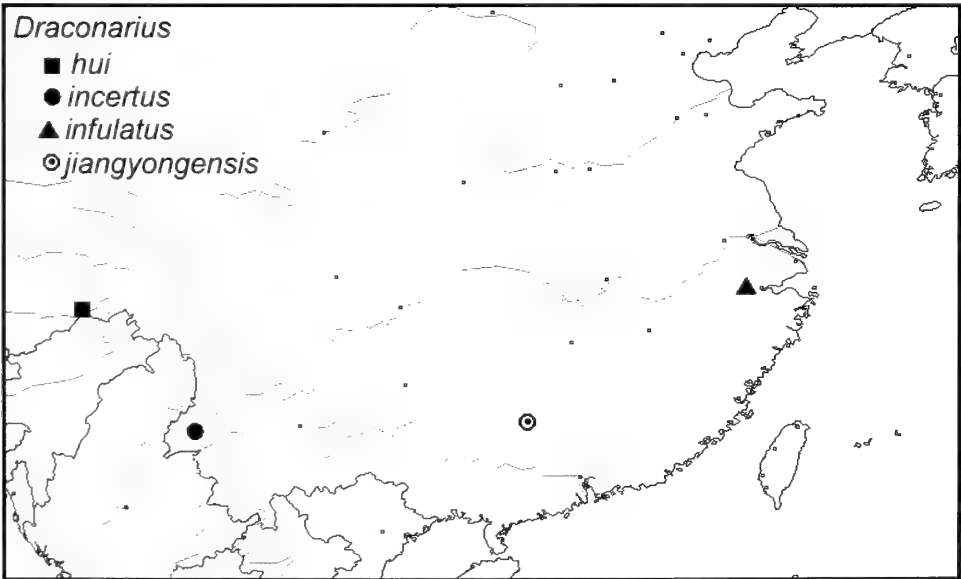


MAP 10. East Asia, showing distribution of *Draconarius episomos*, *D. gurkha*, *D. gyriniformis*, and *D. haopingensis*.

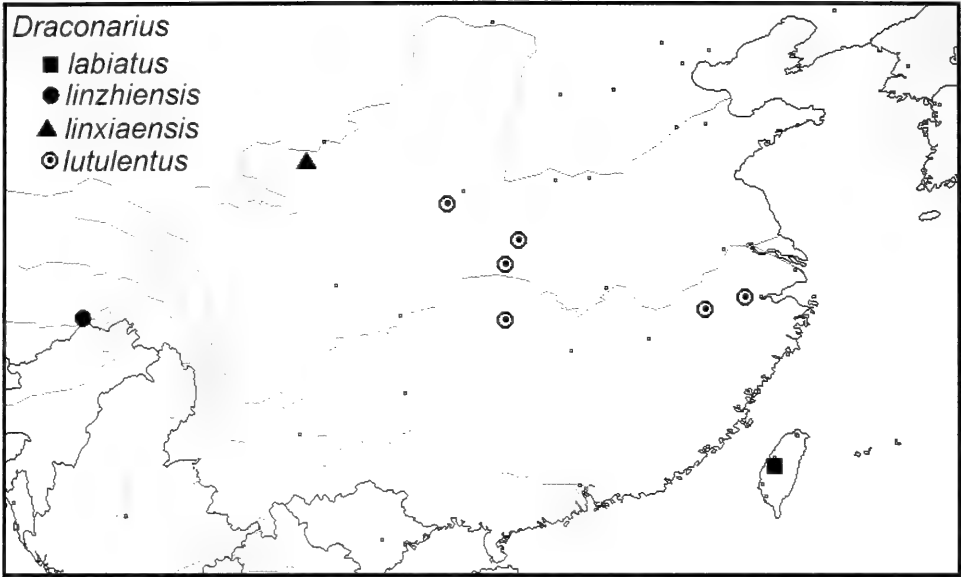




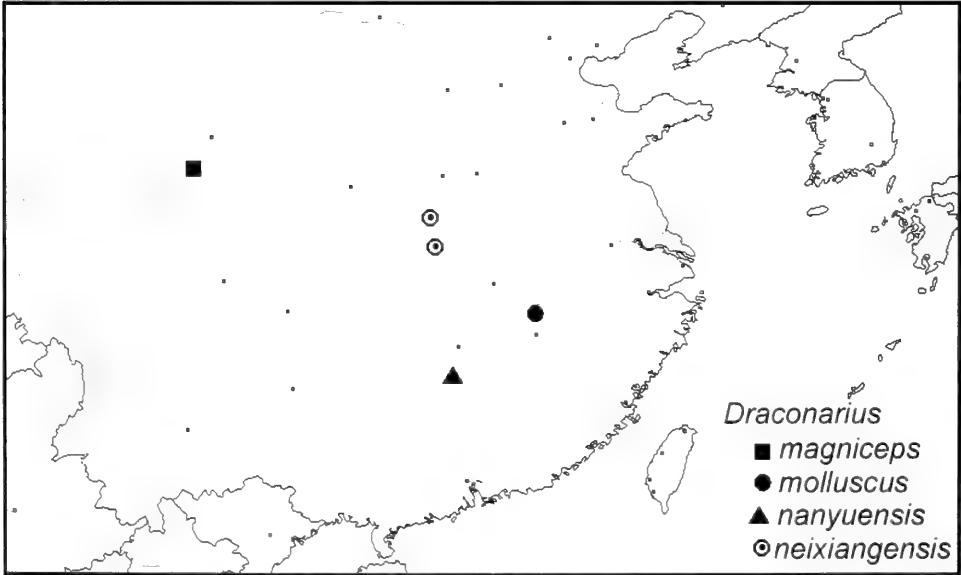
MAP 11. East Asia, showing distribution of *Draconarius griswoldi*, *D. hangzhouensis*, *D. himalayaensis*, and *D. huizhunesis*.



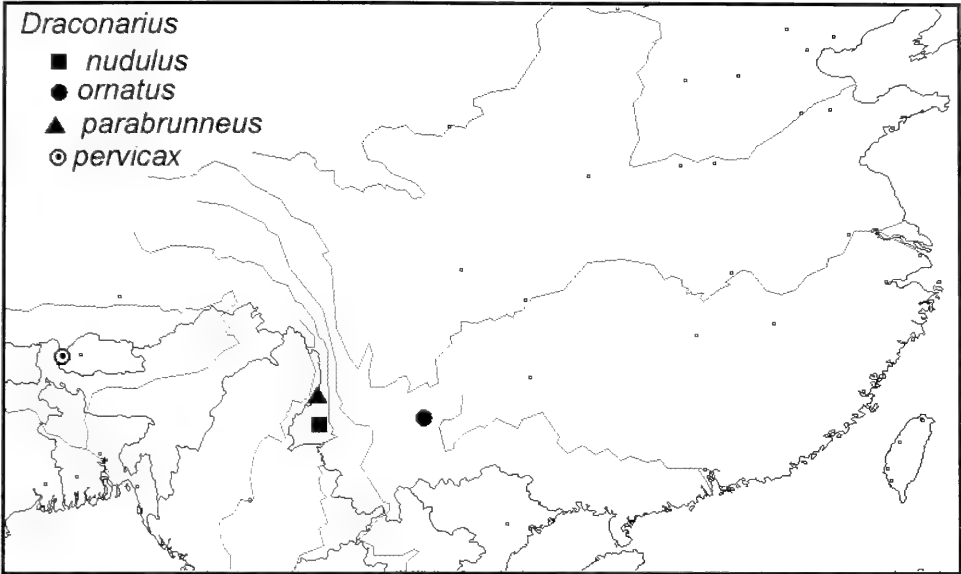
MAP 12. East Asia, showing distribution of *Draconarius hui*, *D. incertus*, *D. infulatus*, and *D. jiangyongensis*.



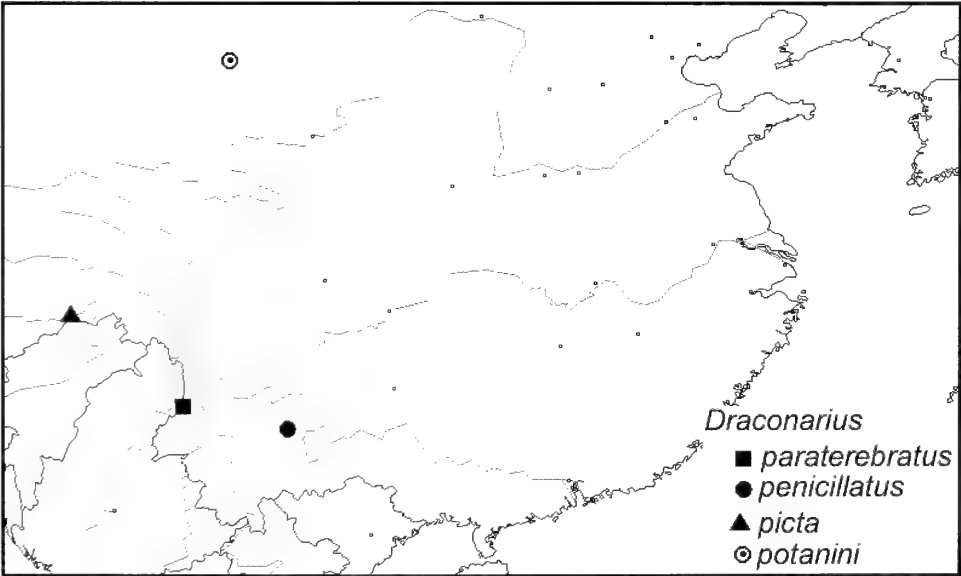
MAP 13. East Asia, showing distribution of *Draconarius labiatus*, *D. linzhiensis*, *D. linxiaensis*, and *D. lutulentus*.



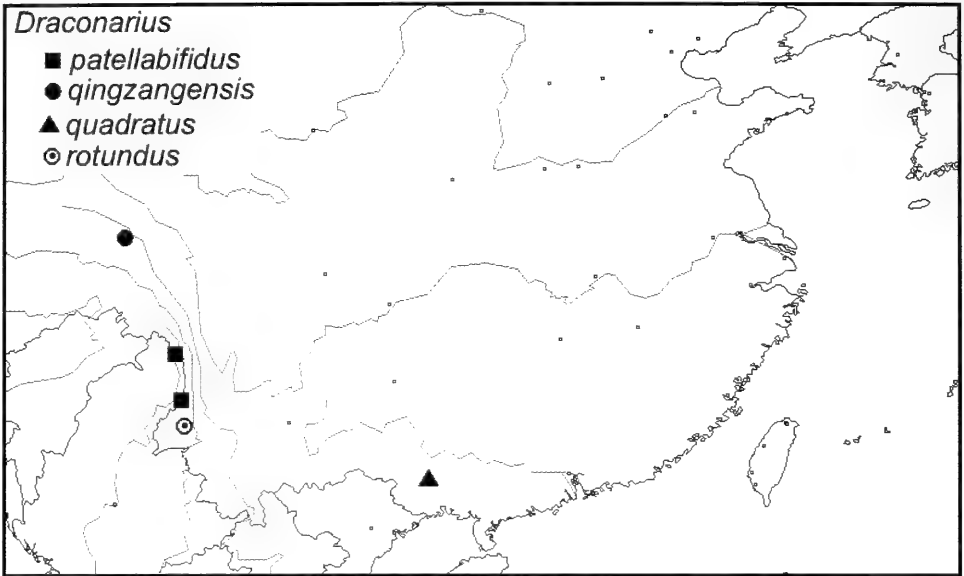
MAP 14. East Asia, showing distribution of *Draconarius magniceps*, *D. molluscus*, *D. nanyuensis*, and *D. neixiangensis*.



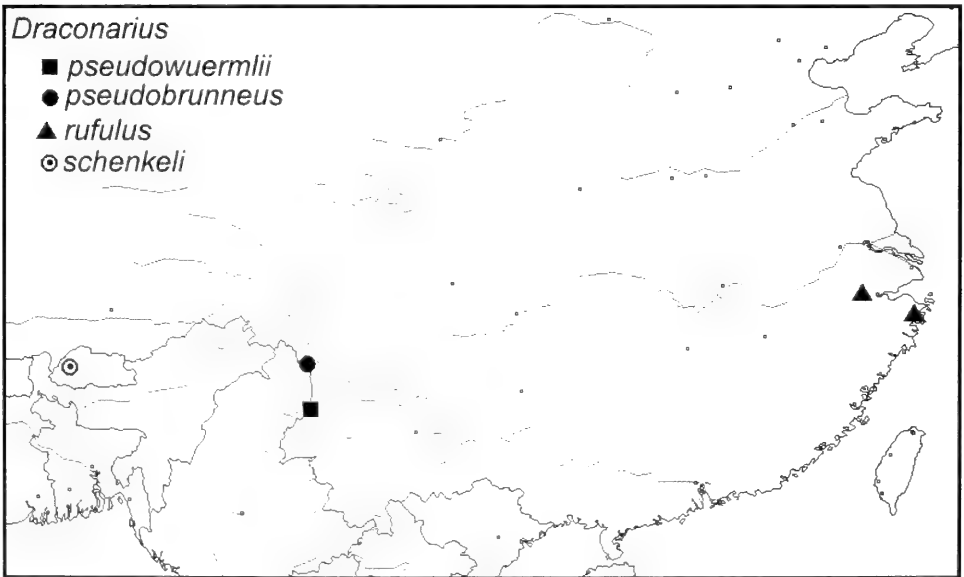
MAP 15. East Asia, showing distribution of *Draconarius nudulus*, *D. ornatus*, *D. parabrunneus*, and *D. pervicax*.



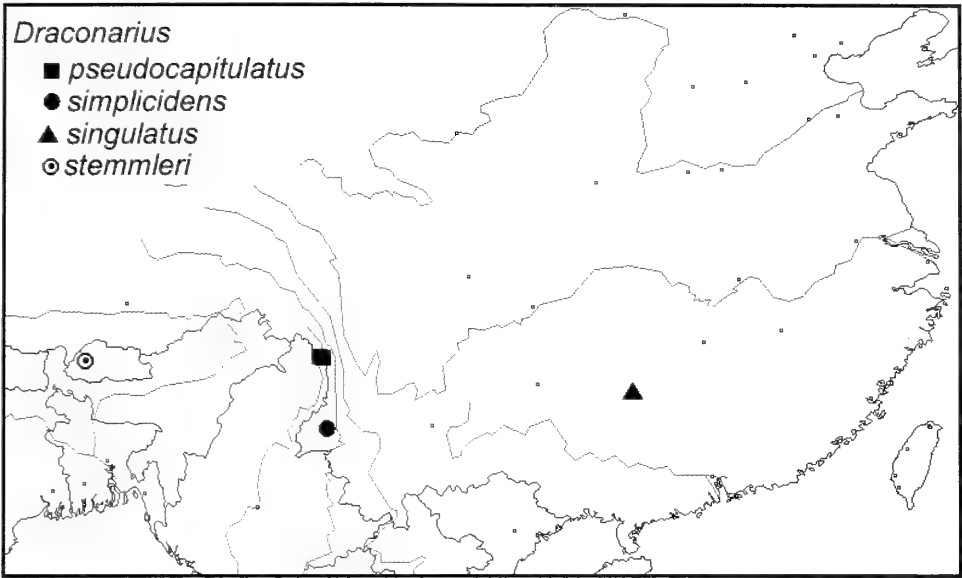
MAP 16. East Asia, showing distribution of *Draconarius paraterebratus*, *D. penicillatus*, *D. picta*, and *D. potanini*.



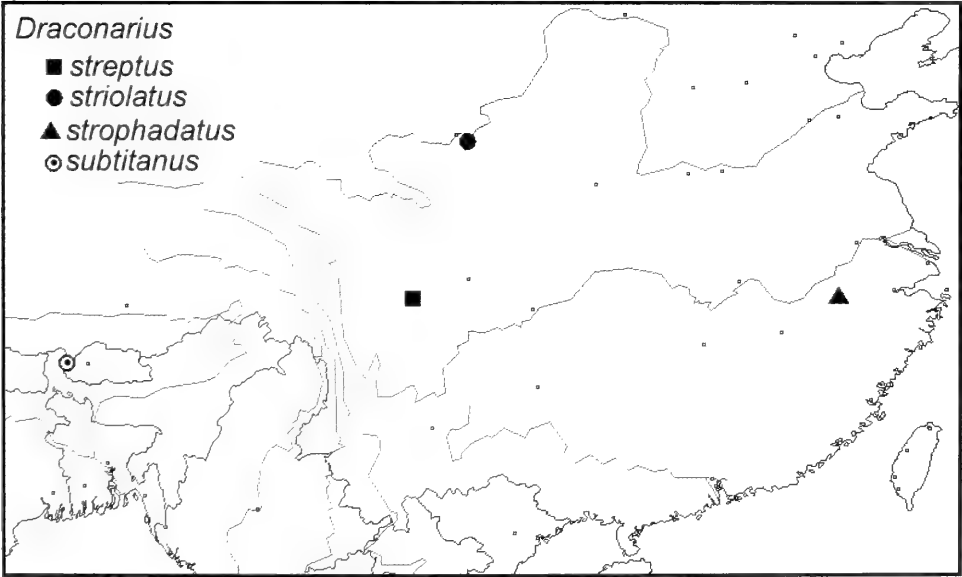
MAP 17. East Asia, showing distribution of *Draconarius patellabifidus*, *D. qingzangensis*, *D. quadratus*, and *D. rotundus*.



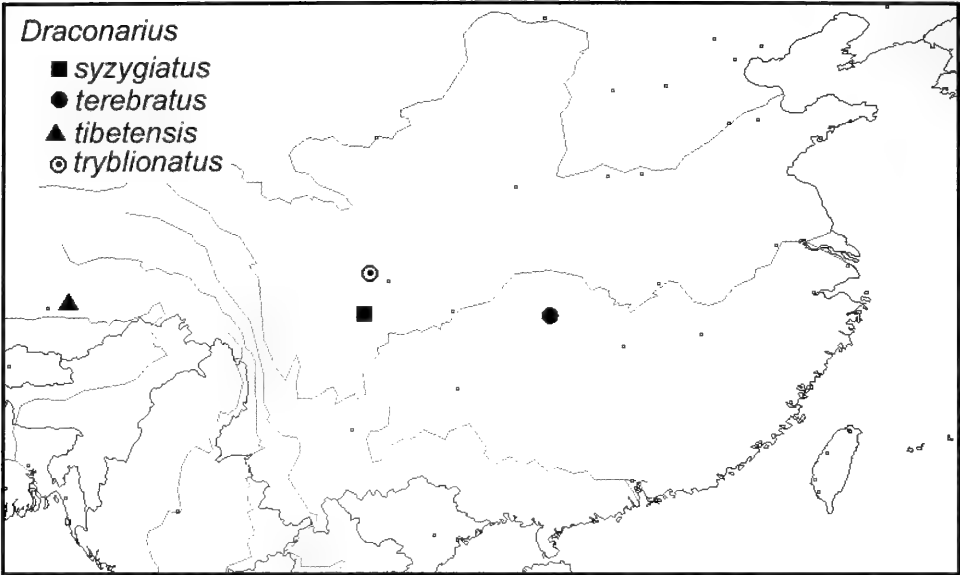
MAP 18. East Asia, showing distribution of *Draconarius pseudowuermlii*, *D. pseudobrunneus*, *D. rufulus*, and *D. schenkeli*.



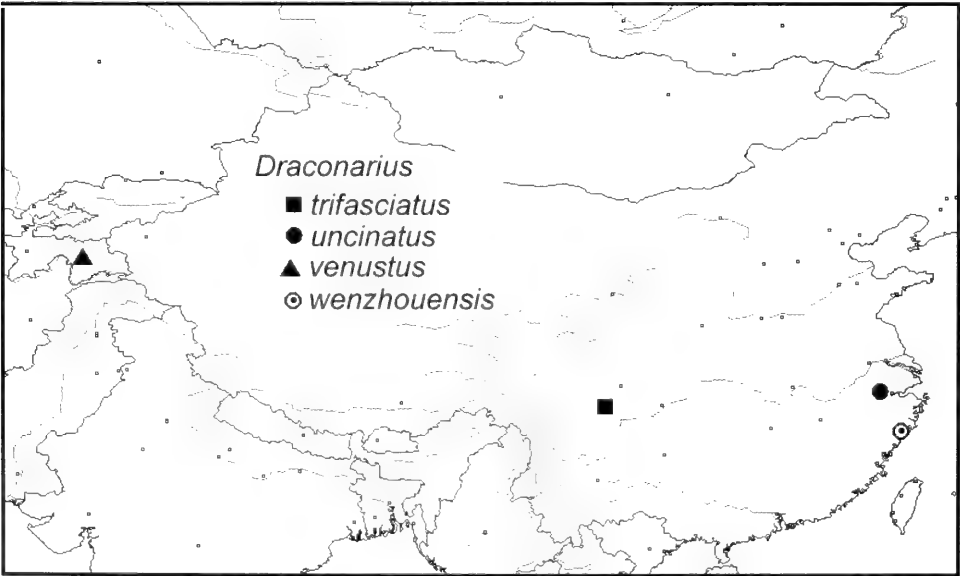
MAP 19. East Asia, showing distribution of *Draconarius pseudocapitulatus*, *D. simplicidens*, *D. singulatus*, and *D. stemmleri*.



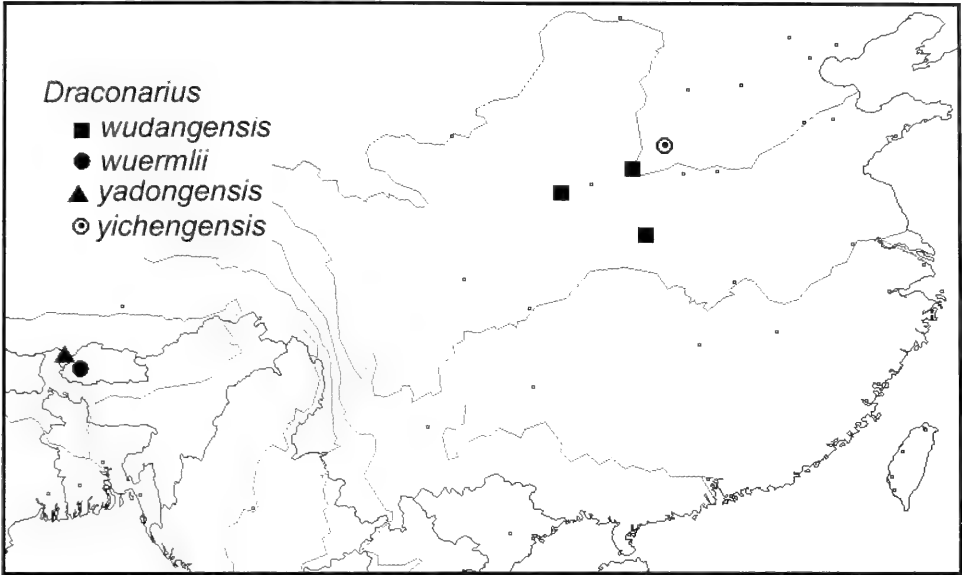
MAP 20. East Asia, showing distribution of *Draconarius streptus*, *D. striolatus*, *D. strophadatus*, and *D. subtitanus*.



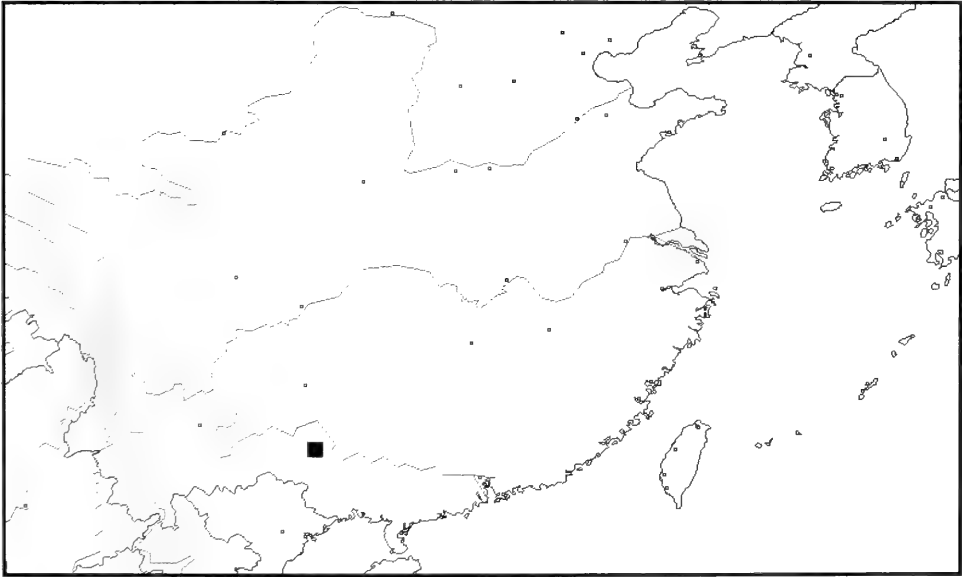
MAP 21. East Asia, showing distribution of *Draconarius syzygiatus*, *D. terebratus*, *D. tibetensis*, and *D. tryblionatus*.



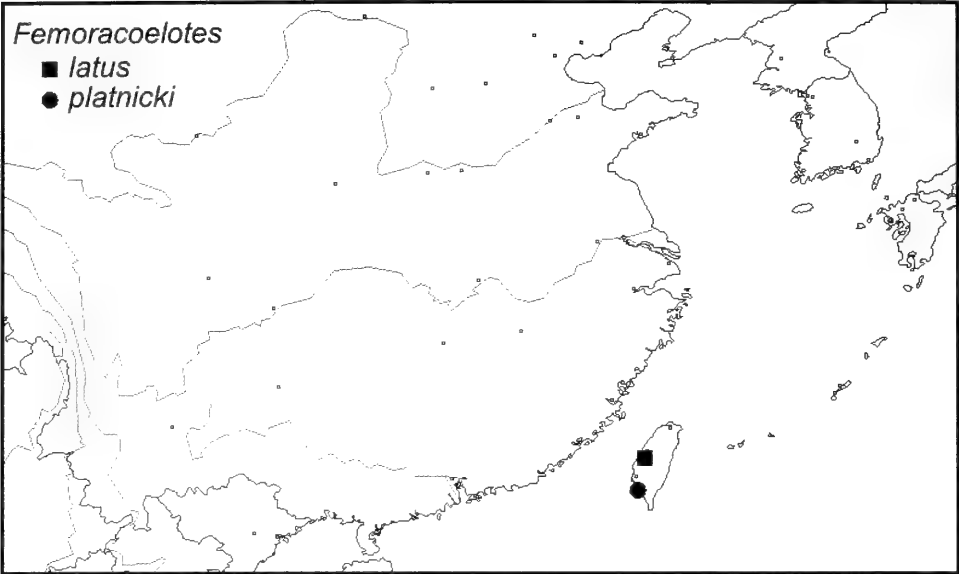
MAP 22. East Asia, showing distribution of *Draconarius trifasciatus*, *D. uncinatus*, *D. venustus*, and *D. wenzhouensis*.



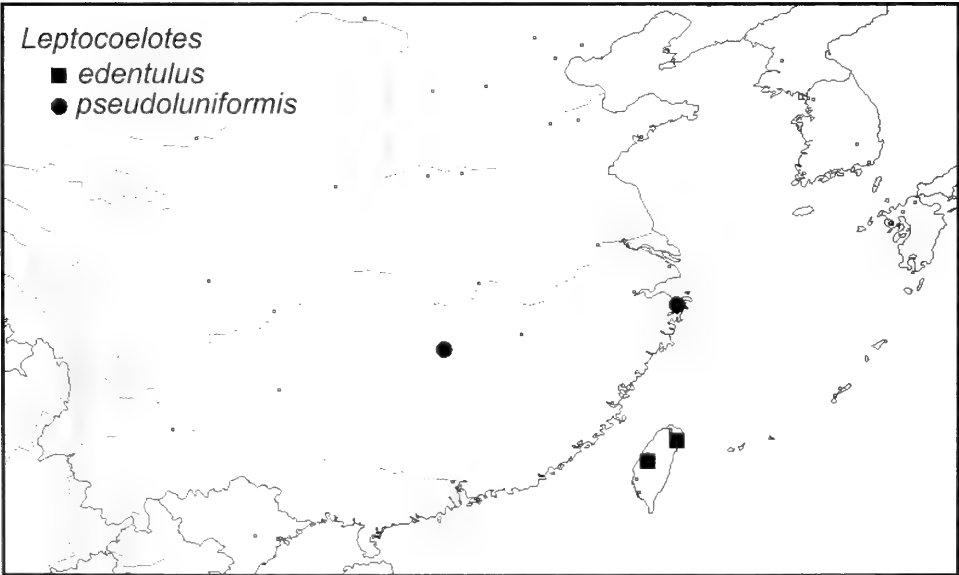
MAP 23. East Asia, showing distribution of *Draconarius wudangensis*, *D. wuermlii*, *D. yadongensis*, and *D. yichengensis*.



MAP 24. East Asia, showing distribution of *Draconarius yosii*.

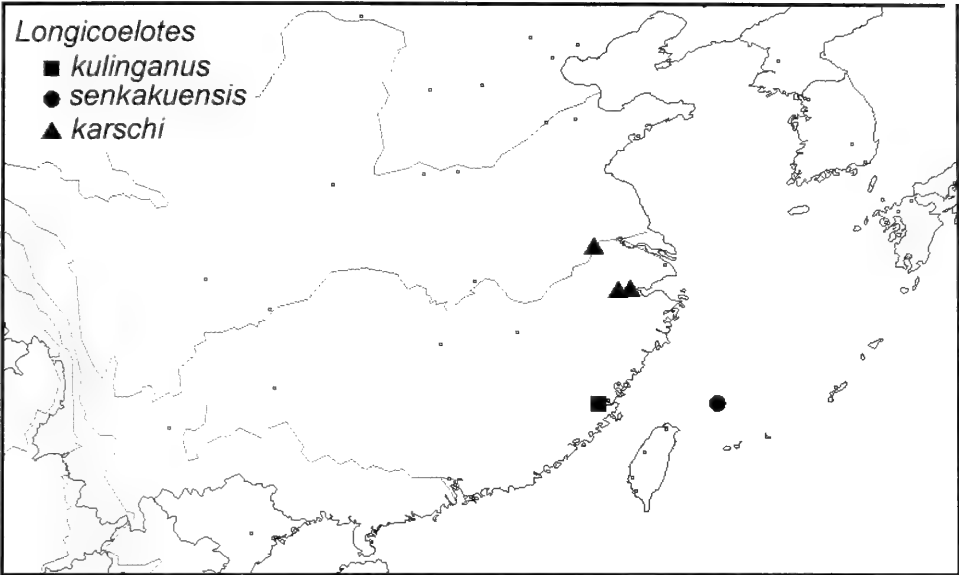


MAP 25. East Asia, showing distribution of *Femoracoelotes latus* and *F. platnicki*.

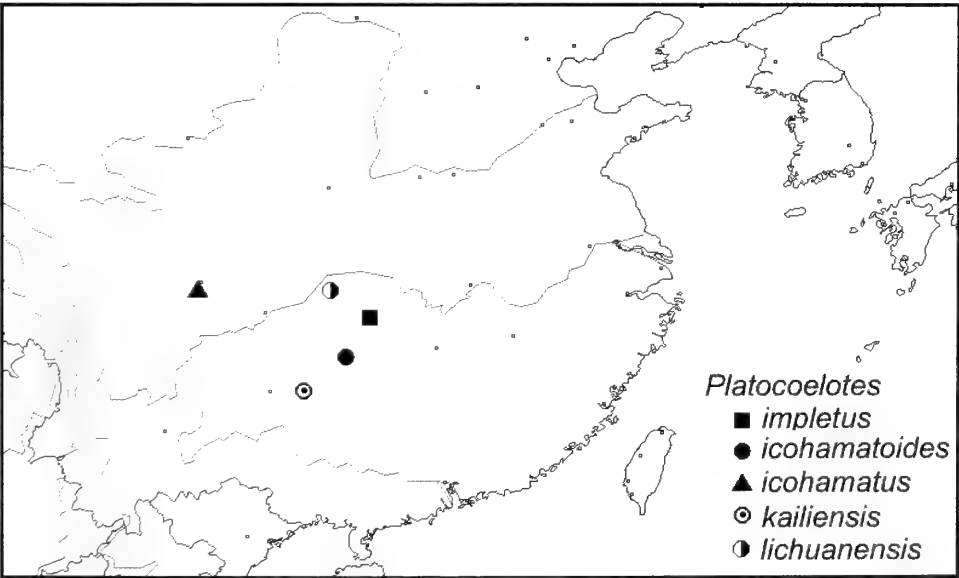


MAP 26. East Asia, showing distribution of *Leptocoelotes edentulus* and *L. pseudoluniformis*.

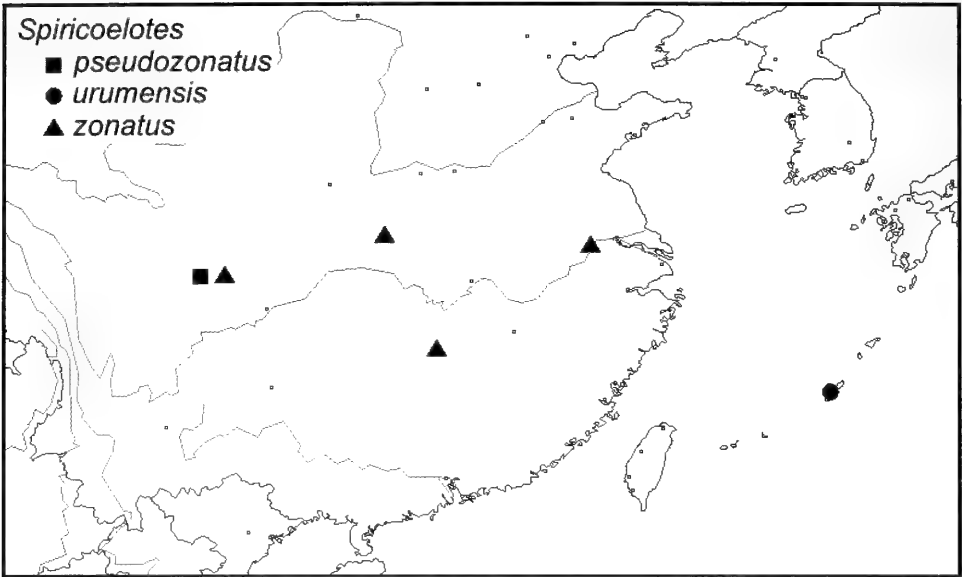




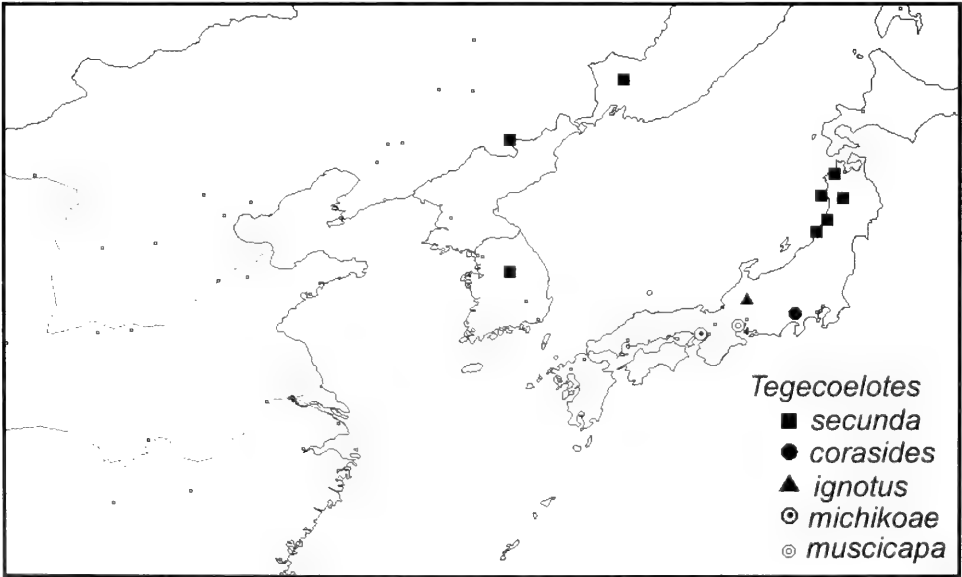
MAP 27. East Asia, showing distribution of *Longicoelotes karschi*, *L. kulianganus*, and *L. senkakuensis*.



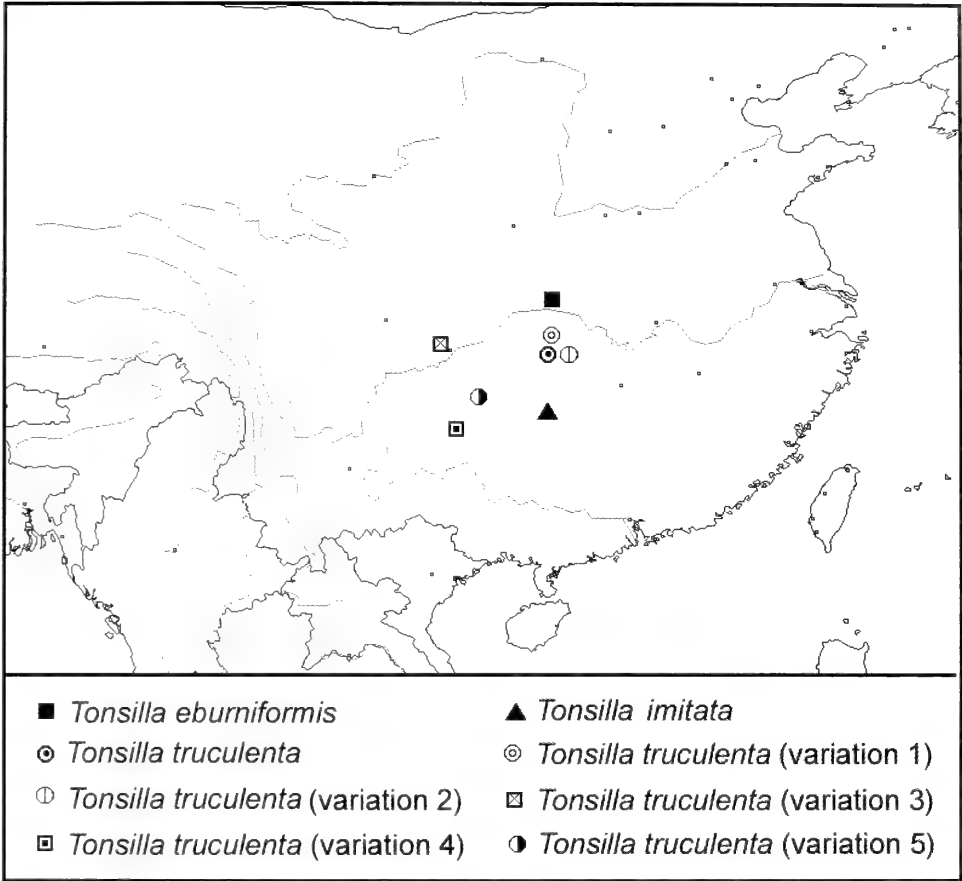
MAP 28. East Asia, showing distribution of *Platocoelotes impletus*, *P. icohamatoides*, *P. icohamatus*, *P. kailiensis*, and *P. lichuanensis*.



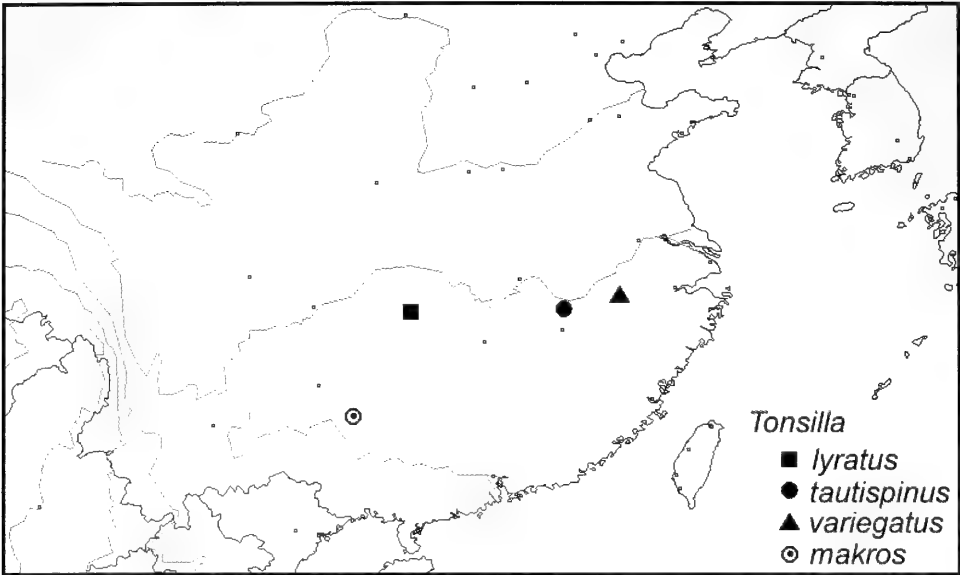
MAP 29. East Asia, showing distribution of *Spiricoelotes pseudozonatus*, *S. urumensis*, and *S. zonatus*.



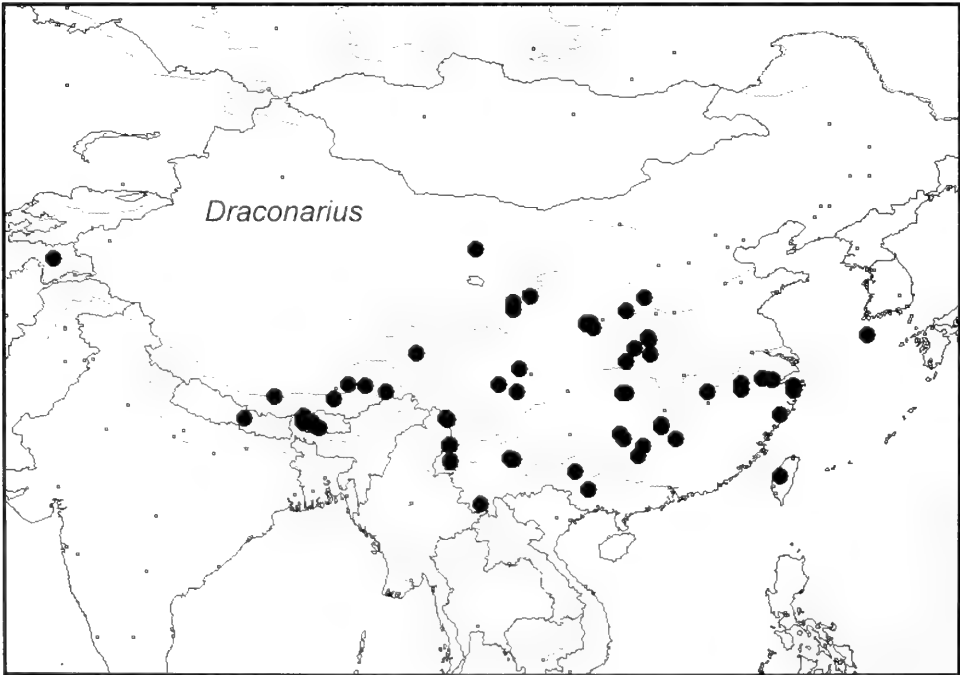
MAP 30. East Asia, showing distribution of *Tegecoelotes secunda*, *T. corasides*, *T. ignotus*, *T. michikoeae*, and *T. muscipapa*. (the distribution site data are incomplete)



MAP 31. East Asia, showing distribution of *Tonsilla eburniformis*, *T. imitata*, and *T. truculenta*.



MAP 32. East Asia, showing distribution of *Tonsilla lyratus*, *T. tautispinus*, *T. variegatus*, and *T. makros*.



MAP 33. East Asia, showing distribution of *Draconarius*.

## Fact, Theory and Tradition in the Study of Molluscan Origins

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Discussions of phylogenetic relationships and origins often use figures called “archetypes,” or “reconstructed common ancestors.” Here we discuss one such creature, the hypothetical ancestral mollusc or HAM. HAM first appeared 150 years ago as T.H. Huxley’s archetypal mollusc and has speciated often since then. Radiations have occurred within both fossil and Recent taxa (from the paleontological and neontological literature, respectively). Eight species have appeared in the last 30 years alone and at least six species remain extant today.

We performed both phenetic and cladistic analyses of the character states present in these figures. Our best approximation of the phylogeny of HAM (based on known ancestor-descendant relationships and stratigraphy) requires 53 more steps than the most parsimonious tree found by cladistic analysis. Phenetic trees based on neighbor joining and UPGMA analyses require two and twelve more steps, respectively than the most parsimonious trees. The evolution of HAM exhibits all the typical processes and developmental heterochronies thought to encompass organic morphological evolution, and both phenetic analysis and cladistic analyses have problems relating paedomorphic taxa.

HAM has not aided evolutionary biologists or paleontologists in solving problems, but it has often had the opposite effect, by requiring that theories be treated within its framework. Moreover, real data have ended up being “tested” against a hypothetical anatomy to determine whether a hypothesis should be accepted or rejected. It has been argued that HAM serves a valuable role as a pedagogical teaching aid. Unfortunately, these imaginary animals do not come clearly labeled with warnings about the harm that they might do if mistaken for real organisms.

*Key words:* Mollusca; hypothetical ancestors; phylogeny; archetypes; typology; conceptual evolution.

According to the current evolutionary ontology, species, lineages, and many other things are individuals, not classes (Ghiselin 1974, 1997; Hull 1976). This suggests that at least some of those “other things” might be studied from an evolutionary point of view. Among the candidates have been sport cars (Rowland 1968), literary genres (Ghiselin 1980), cladists (Carpenter 1987), and scientific theories (Hull 1988). The list could be greatly expanded. One intriguing possibility is lineages of diagrams in the scientific literature. Griesemer and Wimsatt (1989) examine the diagrams that illustrate the Weismannian concept of the continuity of the germ plasm and discuss the study of such diagrams in considerable depth. As they point out, such diagrams can be dated precisely,

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are a very convenient focus of attention, and the analogy between a given diagram and an organism that forms part of a lineage is captivating.

Here we consider some diagrams that depict something even more strongly analogous (and perhaps in a certain sense homologous) to organisms: pictures of hypothetical ancestral molluscs that adorn (one might prefer to say disfigure) the pages of the scientific literature. Our study differs from that of Griesemer and Wimsatt by incorporating phenetic and cladistic analyses to estimate the relationships and character transformations of the images. Furthermore, we direct our commentary primarily to comparative biologists and paleobiologists like ourselves, though we hope that historians and philosophers of science will find it useful as well.

Discussions of phylogenetic problems often use figures called “archetypes,” “*Baupläne*,” or “reconstructed common ancestors.” There is some disagreement as to what such diagrams are supposed to mean. Idealistic morphologists, such as Remane (1952) have asserted that they are just diagrams of the relative position of parts, designed, perhaps, to look like animals. Others, such as Beklemischew (1969), have claimed that, if done properly, they really do represent the common ancestor. From the point of view of taxonomy, we might consider them “pictorial diagnoses”—summaries of the features common to all the organisms in a taxon. From the point of view of phylogenetics, we might consider them hypotheses about a common ancestor—illustrating what was inferred to be present in the last common ancestor of the group. These interpretations are not mutually exclusive.

Systematists often treat hypotheses about common ancestors as results, rather than as starting points, of investigations. To do so makes sense only in terms of a naive inductionism that does no justice to the subtleties of scientific reasoning. Hypotheses are conjectures that are tested by reference to evidence, perhaps by refuting them, as suggested by the title of a well-known book by Popper (1962). Whether one is a “refutationist” (who would deny that hypotheses can be verified) or not, a hypothesis remains a hypothesis irrespective of whether one has gathered any evidence that might lead one to prefer it or some alternative.

Hypotheses are tested by means of experiments, or by comparative methods that are of the same basic logical form as experiments. When a hypothesis explains a variety of empirical data and withstands serious attempts at refutation, it is preferable to one that explains less or generates false predictions about the material universe. With respect to hypothetical ancestral models, this means that at the very least they should have the properties that biologists find among living organisms in general. But the mere plausibility of such a model is no reason to prefer it to some alternative that is equally plausible, or perhaps even more so.

Nonetheless, hypotheses often remain viable in spite of contradictory evidence. There may be some conditions under which it is scientifically legitimate not to falsify a particular hypothesis even when it seems to have been refuted. For example, the test may refute, not the hypothesis itself, but another premise in the system, for example, a “fact” that turns out to be an inaccurate measurement. However, when the hypothesis is simply taken for granted, and contradictory data are ignored or explained away, something is wrong. In this case we are dealing with something that functions not as a hypothesis, but as an assumption being treated as if it were fact. Non-algorithmic phylogenetic hypotheses are often treated this way, but so are many others. The reasons for this are not to be sought in pure logic. Scientists are not alone in accepting what everybody around them takes for granted. They believe what they read in textbooks and what they were told by their teachers. What they accept becomes an integral part of a body of knowledge, in which fact and conjecture are not clearly distinguished. The data then become selectively gathered in a way that tends to “confirm” the assumptions. If unaware of the premises, scientists may be unable to recognize the circularity of their own reasoning. Thus, we get covert assumptions that are better called “tradi-

tions" than "hypotheses," but that are treated as "facts" by their proponents. Only by going back to fundamentals, identifying the premises, and distinguishing fact from theory, can we hope to get outside the circle. The initial premises must be conjectural and open to revision. The notion that one can start out with unbiased data is a preposterous myth.

Traditions, like species, are individuals: they originate, vary, compete with one another, evolve, and, ultimately, become extinct. To come to grips with them, we must deal with them as historical entities, see where they came from, and what forces have maintained them in their environments. Herein we discuss one such creature, Huxley's Archetypal Mollusc — HAM for short. Kept in an artificial, polemic environment, it has flourished and persisted in spite of its teratological character, an animal that never existed except in the fancy of theoreticians.

## MATERIALS AND METHODS

**TAXA STUDIED.**— Our study lineage dates from Huxley (1853) who referred to his special creation as the "archetypal molluscous form" and cautioned that he was not proposing any idealized form. Instead, Huxley viewed his archetype as a starting point on which the "the known laws of development" might act to modify it into "the different secondary types." Thirty years later Lankester (1883) referred to his modification of Huxley's diagram as the "schematic mollusc" in the figure caption. However, within the text Lankester allowed for the possibility that the schematic mollusc might, in fact, represent the "original Mollusc or archi-Mollusc (more correctly Archimalakion)." For consistency we here select Huxley's use of the phrase "archetypal molluscous form" as the first designation, and because of the lack of rules of nomenclature for common names, and as first revisers of HAM nomenclature (neither of which matters), transmute this to "Huxley's Archetypal Mollusc" or HAM, and designate it as the type species and the common ancestor of all taxa placed in the imaginary genus *Hamus*.

Specimens collected in academic libraries provided clear evidence that HAM has speciated often since 1853. At least eight species have appeared in the last 30 years alone and more than six species remain extant today. These species include both fossil and Recent taxa (from the paleontological and neontological literature respectively). Twenty-two taxa were included in the initial analyses; the outgroup taxon and 21 ingroup taxa (Table 1 and Appendix). These taxa were chosen because they represented both neontological and paleontological lineages, and are mostly found in textbooks.

Six additional "Cambrian" species were included in a second analysis. These species have a first occurrence in Pojeta and Runnegar (1976: Figs. 9a-f), and have had a very important role in the discussion of monoplacophoran and gastropod relationships (e.g., Peel 1991; Geyer 1986; Parkhaev 2001). We included them here in a second analysis because fossils can often be extremely important in phylogenetic reconstruction (Donoghue et al. 1989).

**EXCLUDED TAXA.**— We restrict our analysis of taxa primarily to the Anglo-American subclade *Hamus* s.s. Other taxa, belonging to separate intellectual traditions (i.e., lineages) have evolved in relative isolation to the Anglo-American fauna. For example, many of the German language taxa are clearly distinct, the language barrier inducing a certain amount of endemism and reduced opportunities for outbreeding and hybridization although there is some evidence of limited outcrossing on the continent. For example, Haszprunar (1992) published a HAM in an Italian journal and Salvini-Plawen and Steiner (1995) published in an English book (we include *Hamus salvinisteinerorum* in our analysis because of its prominent Anglo habitat). Also see remarks on the relationships of *Hamus pelseneeri*, *Hamus (Jambonus) portmanni* and *Hamus (Schinkenus) naefi* below.

Other taxa such as the peculiar *Protohamus verrilli* developed by Verrill (1896) and

*Protohamus yongi* (Yonge 1960) have been excluded from our analysis. Verrill's species was a larva or "veliger-like form"; an enviable hopeful monster, evidently produced through complete progenetic loss of all adult structures. *P. yongi* is similar to Verrill's creation, although Yonge's later special creations are clearly referable to the genus *Hamus*.

**OUTGROUP AND CHARACTER SELECTION.**— The data available for the study of the evolution of *Hamus* are unique. We possess an almost perfect fossil record for the taxon, preserved in dated textbooks and other publications (Fig. 1; Table 1). We also have the actual common ancestor in its natural environment. The characters are limited to the anatomical features that each author penned into their creature, and the character transformations fixed by our possession of most of the actual phylogeny of the group, often indicated by such expressions as "After. . .", or "Redrawn from . . ." in the caption of the figure. In tracing the various derived forms from their known origin, we can readily observe the character transformations, evolutionary trends and divergences. Moreover, we have an excellent opportunity to test phylogenetic hypotheses (e.g., phenograms and cladograms) with the actual history of the group.

HAM did not arise without antecedents. Traces of its early beginnings can be found in the writings of von Baer (1828:pl. 3, fig. 12). However, as a clearly recognizable entity (i.e., an individual), from which the others were derived, it takes its origin from a drawing by T.H. Huxley (1853) (Fig. 2). Therefore, *Hamus huxleyi* is the consummate sister taxon and outgroup.

The ancestral condition exhibited by *Hamus huxleyi* provides the plesiomorphic states for characters used in our analysis (Fig. 2; Appendix). These character states include a body with clearly differentiated head and foot, cephalic and optic tentacles, and a dorsal visceral mass covered by a mantle. Surprisingly, a shell is absent. The viscera consist of a straight digestive tract with a style sac, a heart with an anterior aorta, and paired kidneys. Gills are present on the postero-dorsal surface of the animal. It is important to note that in the ancestral condition the gills are not located in a posterior mantle cavity. The *H. huxleyi* nervous system consists of four major pairs of ganglia (cerebral, pleural, pedal, and buccal). Obviously Huxley had a rather snail-like ancestor in mind — a sort of untorted limpet without a shell. It stands to reason that when one thinks typologically one will associate "the mollusc" with the most familiar examples, rather than with creatures that are more exotic such as chitons or scaphopods.

**ANALYSIS.**— The character matrix and analysis (see Appendix) describes the 36 characters used in our analyses and their states. We performed both phenetic and cladistic analyses of the data using PAUP\* Ver. 4.0b10 (Swofford 1998). The UPGMA and neighbor joining options in PAUP\*

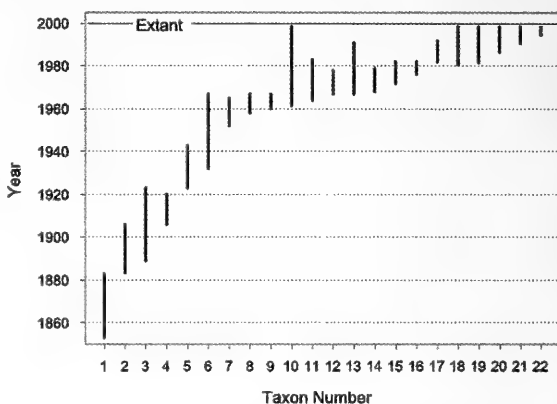


FIGURE 1. Stratigraphic distribution of *Hamus* species treated herein. Taxa 10 and 18–22 are currently extant. Taxon numbers are referenced to Table 1.

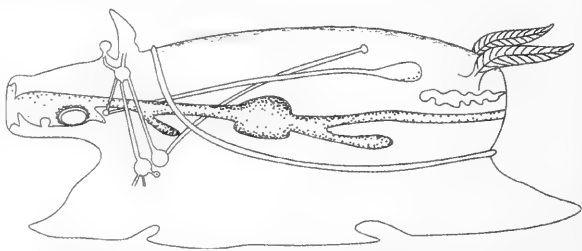


FIGURE 2. *Hamus huxleyi*. T.H. Huxley's Archetype of the Cephalous Mollusca. Redrawn from Huxley (1853).



TABLE 1. Data for *Hamus* species analyzed here. Citations for figured specimens consists of Author(s) + First columns. Data present below are also graphically represented in Figure 1 (First and Last occurrences) and Figure 8a (Duration).

<i>Taxon</i> <i>No.</i>	<i>Taxon</i>	<i>Author(s)</i>	<i>First</i>	<i>Last</i> <i>(to 2000)</i>	<i>Duration</i>	<i>Paleo</i>	<i>Textbooks</i>	<i>Insular</i>
1	<i>H. huxleyi</i>	Huxley	1853	1883	30			√
2	<i>H. lankesteri</i>	Lankester	1883	1906	23			√
3	<i>H. nicholsoni</i>	Nicholson & Lydekker,	1889	1923	34	√	√	√
4	<i>H. pelseneeri</i>	Pelseneer	1906	1920	14		√	√
5	<i>H. swinnerton</i>	Swinnerton	1923	1943	20	√	√	√
6	<i>H. borrapottorum</i>	Borradaile & Potts	1932	1967	35		√	√
7	<i>H. moolafisherorum</i>	Moore, Lalicker & Fisher	1952	1965	13	√	√	
8	<i>H. mortoni</i>	Morton	1958	1967	9			√
9	<i>H. eastoni</i>	Easton	1960	1967	7	√	√	
10	<i>H. barnesi</i>	Barnes	1963	—	37		√	
11	<i>H. mortonyongorum</i>	Morton & Yonge	1964	1983	19			√
12	<i>H. hickmani</i>	Hickman	1967	1978	11		√	
13	<i>H. meglitschi</i>	Meglitsch	1967	1991	24		√	
14	<i>H. russellhunteri</i>	Russell-Hunter	1968	1979	11		√	
15	<i>H. staseki</i>	Stasek	1972	1982	10			
16	<i>H. yongethompsonorum</i>	Yonge & Thompson	1976	1982	6			√
17	<i>H. barthbrosonum</i>	Barth & Broshears	1982	1992	10		√	
18	<i>H. bossi</i>	Boss	1982	—	18			
19	<i>H. seedi</i>	Seed	1983	—	17			√
20	<i>H. barcalolivorum</i>	Barnes, Calow & Olive	1988	—	12		√	√
21	<i>H. ravenjohnsonorum</i>	Raven & Johnson	1992	—	8		√	
22	<i>H. salvinisteinerorum</i>	Salvini-Plawen & Steiner	1996	—	4			

were used to calculate phenetic trees based on distance matrix of mean character differences. In both phenetic analyses ties were broken randomly. The data matrix was also subjected to heuristic searches under maximum parsimony with *H. huxleyi* serving as the outgroup. All characters were equally weighted and unordered, and were assumed to show accelerated character transformation. Strict and majority rule (50%) consensus trees were calculated.

RESULTS

The single tree from the UPGMA analysis is presented in Fig. 3a; it contains two distinct groupings. The first group is made up of the early HAM taxa + pedomorphic taxa + flatworm-like

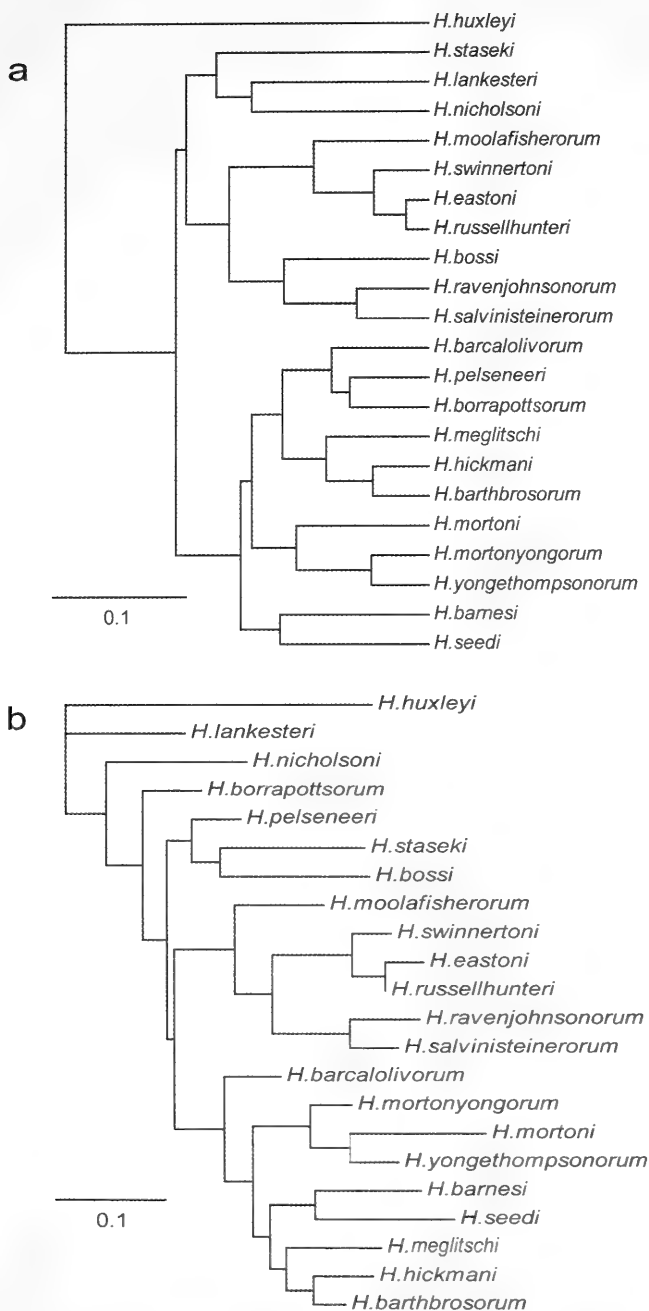


FIGURE 3. Phenetic trees from analysis of distance matrix of mean character differences. a. UPGMA and b. neighbor joining analysis. (See Appendix for data matrix.)

consensus tree (Fig. 4b) is virtually identical to the neighbor joining solution; they differ primarily in the placement of *Hamus mortonyongorum* and *Hamus borrapottorum*. Half of the resolved branches appear in 80% or more of the most parsimonious trees (Fig. 4b).

taxa. Although the paedomorphs + flatworm-like taxa are clearly delimited in the analysis, the disjunct stratigraphic record of these taxa suggests that this cluster is better attributed to convergence rather than common ancestry. The second cluster consists primarily of textbook HAMs + the insular (*i.e.*, British) HAMs. Unlike the first cluster, the textbook and insular HAMs do not form unique groups, but instead are mixed within the cluster. The topology of the UPGMA tree requires 108 steps.

The single tree from the neighbor joining analysis is presented in Fig. 3b. In the neighbor joining analysis, the flatworm-like taxa group with the textbook and insular HAMs with the paedomorph group as its sister taxon. *Hamus lankesteri* and *Hamus nicholsoni* are outside of these three groups in both phenetic analyses. The topology of the neighbor joining tree requires 98 steps.

Maximum parsimony analysis found 76 trees with 96 character steps. Strict and majority rule consensus trees for these trees are presented in Fig. 4. In the strict consensus tree, four subclades are present (Fig. 4a). These are: (1) *Hamus mortoni* and *Hamus yongethompsonorum*, (2) *Hamus pelseneeri* and the flat worm-like HAMs, (3) the paedomorph group, and (4) HAMs from four American invertebrate zoology textbooks and the single insular species *Hamus seedi*. The majority rule

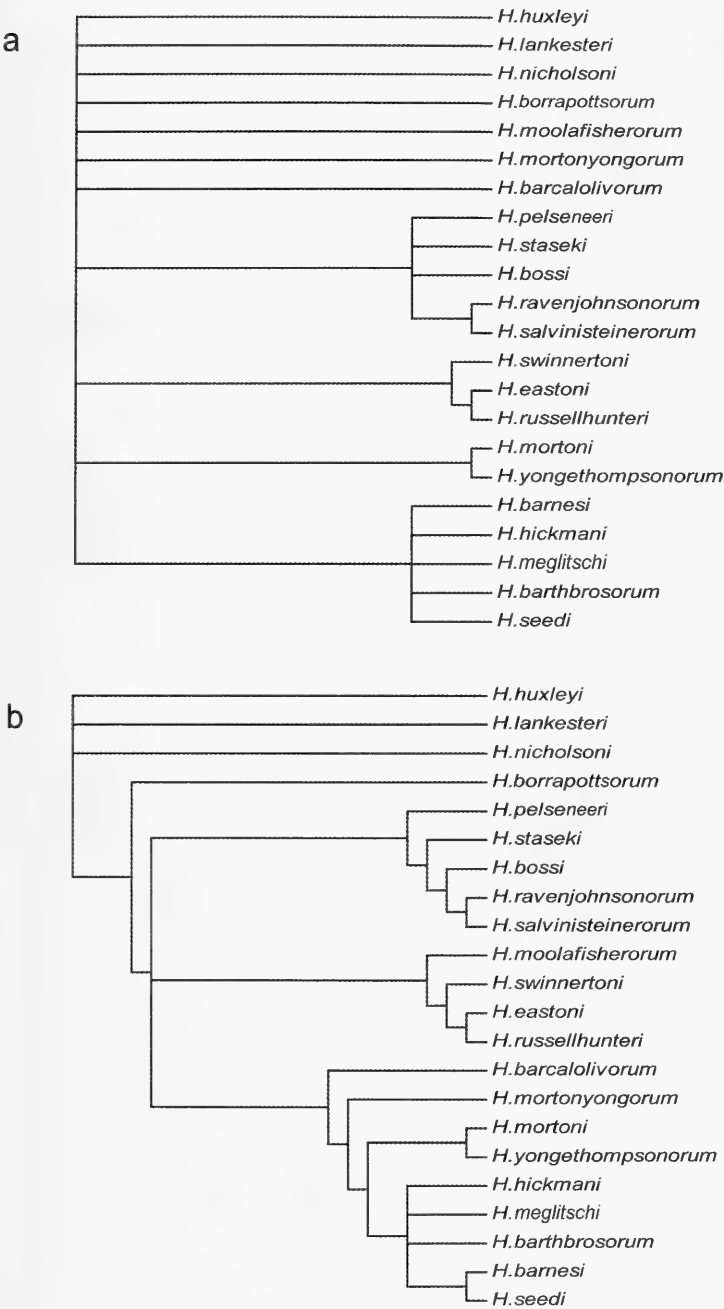


FIGURE 4. Consensus cladograms of 76 most parsimonious trees found by PAUP\* analyses of the 22 HAM taxa listed in Table 1. CI and RI for randomly selected tree (No. 127) = 0.4725 and 0.6000, respectively. a. Strict and b. majority rule consensus trees. (See Appendix for data matrix.)

In the final cladistic analysis, the “Cambrian” species complex *Hamus pojetarunnegarorum*, comprising six taxa, was added to the data matrix. *Hamus pojetarunnegarorum* taxa are well known in the Cambrian literature (e.g., Pojeta and Runnegar 1976) where they are typically used to differentiate between untorted and torted molluscs. Because of their association with some of the oldest molluscan fossils, they have some of the highest number of unknown character states in the analysis, being surpassed only by some of the paedomorphic taxa (see Appendix). The addition of these taxa to the data matrix produced 4875 trees of 1034 character steps. In the strict consensus tree, the addition of these taxa produces a large unresolved polytomy at the base of the tree while the only remaining subclades are *Hamus mortoni* and *Hamus yongethompsonorum* and the HAMs from four American invertebrate zoology textbooks + the single insular species *Hamus seedi* (Fig. 5a). In the majority rule consensus tree (Fig. 5b), the complex is situated in a subclade consisting primarily of paedomorphs with the exception of the flat-worm-like *Hamus ravenjohnsonorum* with which *H.*

*pojetarunnegarorum* taxon groups. The remaining members of the complex form their sister taxon. The overall effect of the addition of fossils to our analysis is to intermingle members of the flat-

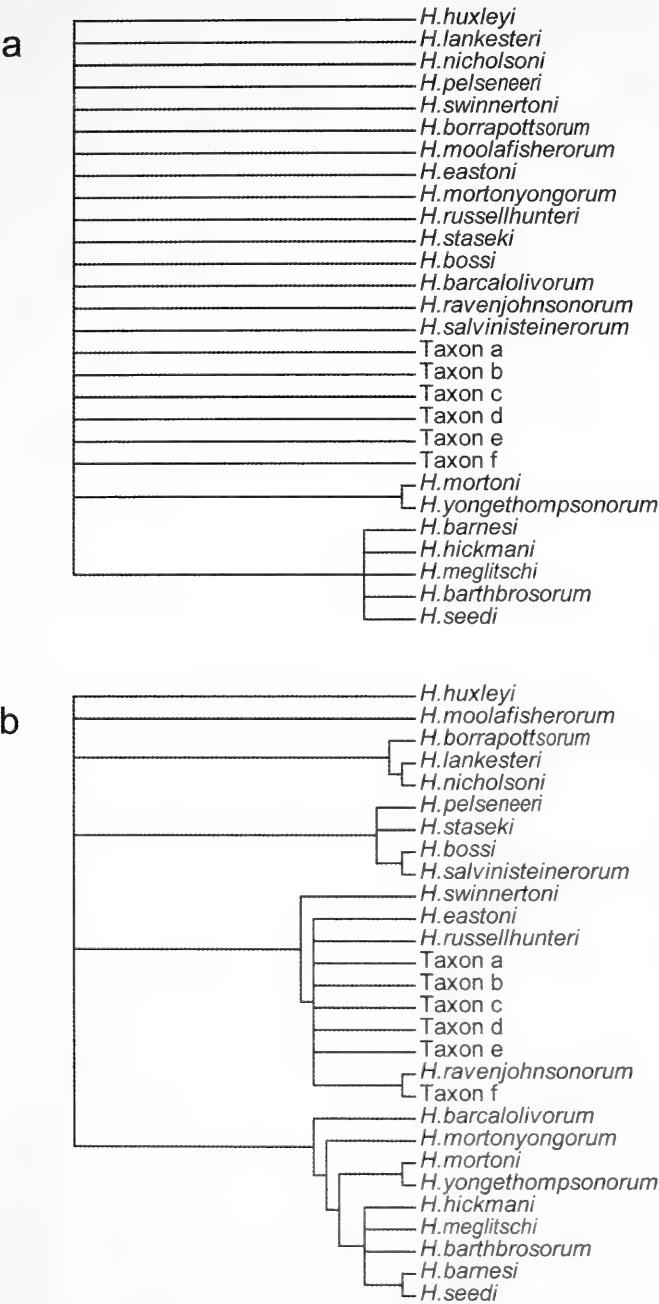


FIGURE 5. Consensus cladograms of 4875 most parsimonious trees found by PAUP\* analyses of the 22 HAM taxa listed in Table 1 plus six taxa of the “Cambrian” species complex *Hamus pojetarunnegarorum*. CI and RI for randomly selected tree (No. 356) = 0.4757 and 0.6932, respectively. a. Strict and b. majority rule consensus trees. (See Appendix for data matrix.)

worm-like and paedomorph groups and reduce overall resolution of these groups. In contrast, occurrence of the subclade consisting of *Hamus mortonyongorum*, *Hamus barcalolivorum*, *Hamus mortoni*, *Hamus yongethompsonorum*, the four American invertebrate zoology textbook HAMs and *Hamus seedi* increases from 68% to 97% at three nodes because of the addition of the fossils (cf. Figs. 4b and 5b).

Our best approximation of the actual phylogeny of HAM based on known ancestor-descent relationships and stratigraphy (Fig. 6) requires 53 more steps than the most parsimonious trees. Three distinctive clades are present in this phylogeny (Fig. 6):

- 1. **Lankester group.**— an early group (1883) of mostly fossil species tracing their ancestry to *Hamus lankesteri*. A single pair of paedomorphs represents the most “derived” taxa within this clade.
- 2. **Morton group.**— a large, comb-like group whose members trace their ancestry to *Hamus mortoni* (1958). This group consists of intermingled insular and textbook *Hamus* species. A second pair of paedomorphs is nested within this clade.
- 3. **Stasek group.**— the sister taxon of the Morton group, and although it shares the same minimum age of divergence (1958) with the Morton group, the earliest known members date from 1972 (*Hamus staseki*). Half of the extant *Hamus* species are members of this group. The continental taxon *H. salvinisteinerorum* is arbitrarily placed in this clade because of its recurrent sister taxon relationship with *H. ravenjohnsonorum* in all analyses with the exception of the addition of the Cambrian taxa.

Two of these groups were

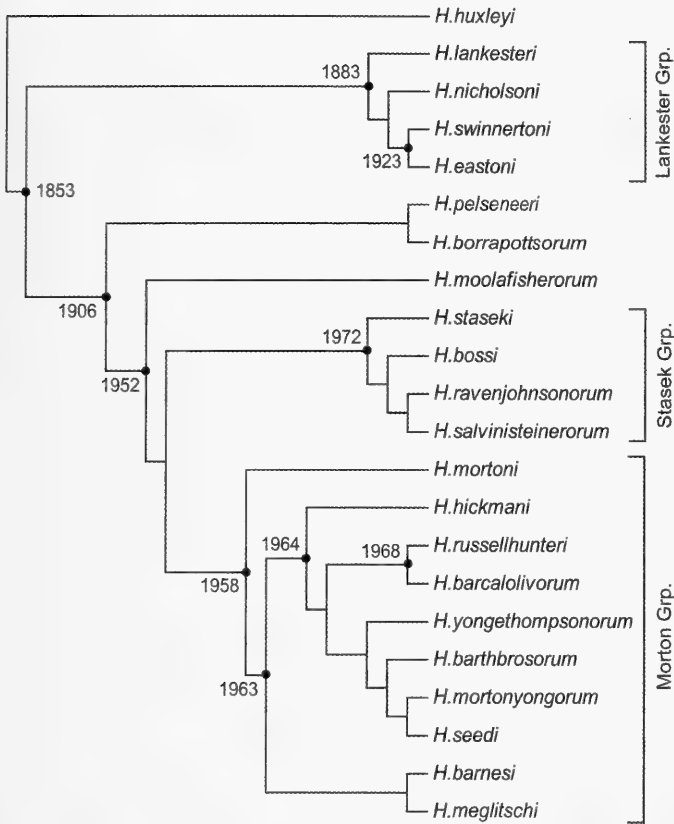


FIGURE 6. Best approximation of the actual relationships of *Hamus* species based on known ancestor-descent relationships and stratigraphy. Dates at nodes indicate minimum divergence times for sister taxa. Consistency index = 0.2986, retention index = 0.1583.

and their anatomies have converged on each other as well as with the fossil taxa (Fig. 5b). However, there is a 45 year difference in the time of origination of the first and most recent of these groups and any suggested relationship is likely to be spurious. The universal occurrence of this group in our analyses shows that whether real organisms or cartoons, paedomorphs are difficult taxa to relate in phylogenetic reconstructions.

**STRATIGRAPHY.**— Fossil HAMs appear earlier in the record than the majority of zoological ones (Fig. 1, Table 1). However, not one fossil HAM has originated in a textbook environment since 1964. In contrast, 76% of zoological HAMs have originated since 1960 and all six of the extant HAMs (*i.e.*, texts and monographs not out of print) are zoological species (Table 1). Before 1960, the ratio between fossil and zoological *Hamus* species was about 1:1 (Table 1).

Following Norell and Novacek (1992) we compared the known stratigraphic ranges with divergence patterns based on our cladistic and phenetic analyses. Testing the fossil record against cladistic phylogenies typically determines how complete the record probably is, and therefore how useful the taxon might be for stratigraphic purposes (Padian et al. 1994). However in our unique situation, the stratigraphy is certain and therefore can be used to evaluate the reconstructed divergence patterns (Fig. 7).

When the number of branch nodes between *Hamus huxleyi* and the taxa on the true tree are

present to varying degrees in our analyses (*cf.* Figs. 3–6). Components of the Morton group are present in the UPGMA and neighbor joining trees, and in both the strict and majority rule consensus cladograms. The Stasek group was represented by the flatworm-like taxa in the UPGMA and neighbor joining analyses, and in the majority rule consensus cladograms. In the UPGMA analysis the Stasek group was the sister taxon of the paedomorph group (Fig. 3a), while in the majority rule consensus cladogram, the neighbor joining tree, and the true phylogeny, this group is the sister taxon of the Morton group (*cf.* Figs. 3b, 4b, and 6).

The “Paedomorph group” which is present in some form in all of our analysis is polyphyletic and represents two separate events, one in the Lankester group and the other within the Morton group. We regard these taxa as paedomorphs because of their degenerated morphology,

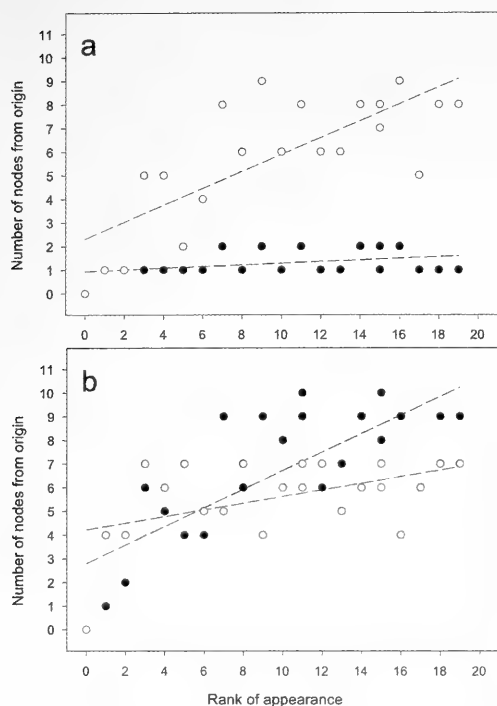


FIGURE 7. Scatterplots of the relationship between rank of appearance (as measured by absolute age) and the number of branch nodes between origin and taxon on tree. a. Results plotted from cladistic analyses. Solid circles from strict consensus cladogram ( $r^2 = 0.1312$ , slope = 0.0335); open circles from majority rule consensus cladogram ( $r^2 = 0.5710$ , slope = 0.3571); b. Results plotted from phenetic analyses. Solid circles from neighbor joining tree ( $r^2 = 0.5900$ , slope = 0.3920); open circles from UPGMA phenogram ( $r^2 = 0.2299$ , slope = 0.1400).

shell, pedal nerve cords, gonads, the movement of the gills into the mantle cavity, and the loss of a differentiated foot, style sac, radula, jaws, aorta, statocysts, epipodium, buccal ganglia, optic tentacles, and buccal mass. This grade in the evolution of *Hamus* (which is generally retained through *Hamus moolafisherorum*) represents a sort of “average” mollusc, with emphasis upon the more “primitive” forms. The basic body plan was arrived at by assuming that characters present in the “most primitive” members of each (extant) class were also present in a common ancestor, and all (extant) classes could be derived from it (see Huxley 1853). Thus, many early *Hamus* species were intended to encompass the characters of the five molluscan classes then known. The discovery of other taxa (such as the fossil Rostraconchia and the still extant Monoplacophora) has done surprisingly little to induce serious rethinking of this original structure (see below).

The only apomorphy of the Lankester group is the appearance of both a posterior and anterior aorta. The HAM of Nicholson and Lydekker (1889) traces its ancestry directly from *Hamus lankesteri*, but shows little of the anatomical retrogression seen in *Hamus swinnertoni* and *Hamus eastoni*. The lack of a radula and gonad in *Hamus nicholsoni* suggests a possible common ancestor, but the lack of tentacles and the cap-shaped shell also suggests a spurious relationship with *Hamus pelseneeri*, which would not make an appearance for another 17 years. A peculiar autapo-

plotted on the rank of appearance of the taxa, the resulting  $r^2$  of the regression equals 0.6746 and the slope equals 0.4223. This is not significantly different from the majority rule consensus tree (Fig. 7a) or the phenetic UPGMA tree (Fig. 7b) (pairwise  $t$ -test,  $p > 0.05$ ). However, it is significantly different ( $p = 0.0012$ ) from the neighbor joining tree regression (Fig. 7b). The strict consensus tree has virtually no stratigraphic signal with a slope of 0.0345 (Fig. 7a).

Origination rates remained below 0.15 species/year for the first 80 years of Hammian history, however between 1960 and 1980 origination rates skyrocketed to over 0.40 species/year and have since begun to decline (Fig. 8a). Extinction rates have typically been lower, but follow a similar trend (Fig. 8a). The consequence of the difference between these two rates is a roughly exponential species diversity curve through time (Fig. 8b). Although species diversity was  $\leq 2$  for over 100 years, the substantially higher origination rates have maintained a relatively stable diversity of five or more HAMs for the last 30 years (Fig. 8b). Lastly, mean duration for individual *Hamus* species is  $16.8 \pm 9.4$  years and the relative frequency of species durations is skewed towards shorter durations (Fig. 8a).

**RELATIONSHIPS AND EVOLUTIONARY SCENARIO.**—Members of the ingroup are derived from *Hamus huxleyi* by the acquisition of a

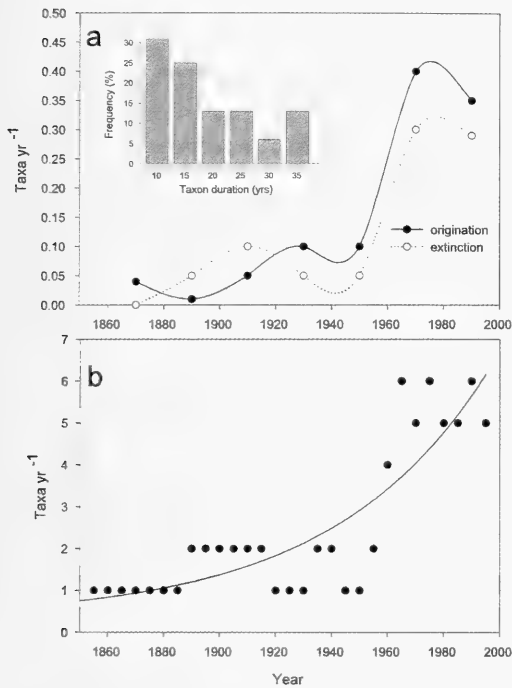


FIGURE 8. Macroevo-lutionary data for *Hamus*. a. extinction and origination rates, and species duration; b. species diversity.

loss of eyes. This basic body plan was arrived at by assuming that the characters are present in most of the remaining taxa with the exception of members of the Stasek group. Something analogous to “species selection” may help to explain why Pelseneer’s HAM had such a strong influence on Anglo-American HAM speciation. Pelseneer was a Belgian and wrote mostly in French, but *H. pelseneeri* appeared in a very influential textbook in English in 1906. Actually, this was a punctuational event in a marginal habitat — Pelseneer (1897) published an earlier version in French. Pelseneer’s HAM species also had an important dispersal episode. Pelseneer (1885) remarks that he worked in Lankester’s laboratory during the winter of 1884–1885, thereby allowing us to document not only direct ancestry, but perhaps the original dispersal event between England and the continent as well. The HAM of Moore, Lalicker, and Fischer (1952) (*Hamus moolafisherorum*) is diagnosed by ventral digestive glands, and the loss of the pericardium, gonads and pedal nerve cords.

The remaining HAMs are divided into two distinct subclades, and it is this divergence between 1952 and 1958 that marks the beginning of the modern *Hamus* radiation (Fig. 6). Before this branching point, the phylogeny of HAM was primarily comb-like (Fig. 6), the earlier HAMs forming a grade of evolution. The synapomorphies that united these two subclades are the presence of the osphradium and radula. Three synapomorphies diagnose the Morton group; all are typical gastropod characters. They include the presence of a style and gastric shield, osphradium, and afferent gill membrane. The five synapomorphies that diagnose the Stasek group are the reappearance of gonoducts, osphradium positioned on dorsal surface of pallial cavity, multiple shell attachment muscles, and the loss of cephalic tentacles and the digestive gland.

Like *Hamus swinnertoni* (Fig. 9a) the HAMs of Russell-Hunter (1968) (Fig. 9c) and Barnes,

morphology characterizes *Hamus nicholsoni* — the anterior mantle cavity with its single branchia (Fig. 10b). This untorted mollusc with an anterior mantle cavity would be a “hopeful monster” in anyone’s phylogeny, and although it might have served as a novel preadaptation for the Gastropoda, it never produced any descendants. The HAM illustrated by Swinnerton (1923) is directly descended from *H. lankesteri* (“after Lankester”) and is the first instance of pedomorphosis in the taxon *Hamus*. *Hamus swinnertoni* (Fig. 9a) has lost numerous organs, including the radula, gonad, heart, pericardium, kidneys, and the entire nervous system. Moreover, the shell of this species is conical rather than cap-shaped, and the overt morphology is distinctively gastropod-like, in spite of its degenerate viscera. *Hamus eastoni* is the sister taxon of *H. swinnertoni* and is even more degenerate (Fig. 9b).

The common ancestor of *Hamus pelseneeri* and *Hamus borrapottorum* is further characterized by the movement of the digestive gland from the ventral to dorsal position, gonads opening into the pericardium, and the

Calow and Olive (1993) are undoubtedly products of paedomorphic processes that have beset these species, and as with so many cases of degenerative evolution, we have at least two cases of convergence amongst four taxa. While the known phylogeny of *H. swinnertoni* allows us to identify its ancestry, we have no indisputable evidence for the determination of the relationships of the remaining three species. However, mentorship distribution and stratigraphy provide insights into their relationships (see discussion of the Morton group below).

The HAMs of Stasek (1972), Boss (1982), Raven and Johnson (1992) (Fig. 9d) and Salvini-Plawen and Steiner (1996) are all flatworm-like. In addition, the solid shell is lost and replaced by a spicule-studded integument in *Hamus bossi*, *Hamus ravenjohnsonorum*, and *Hamus salvini-steinerorum*.

The appearance of the Morton Group marks a major evolutionary event within the genus (Fig. 6). Members of the Morton group have the most complicated anatomies of any of the *Hamus* species, emphasize gastropod features, and mark a clear departure from previous HAM lineages. This increasing convergence with the Gastropoda is clearly illustrated by the sequence a→b→c→d in Fig. 10 (see also Haszprunar 1992).

*Hamus mortoni* is diagnosed by six autapomorphies (jaws, two digestive glands, epipodial tentacles, salivary glands, esophageal glands, and spherical kidneys), all of which further emphasize gastropod features. Many features present in the gastropod-like *H. mortoni* are absent in the Morton and Yonge (1964) HAM. *Hamus mortonyongorum* has lost the osphradium, afferent gill membrane and eyes. The nervous system is also condensed, and only a single ganglion remains.

Two American HAMs are basal members of the Morton group — *Hamus barnesi* (Barnes 1963) and *Hamus meglitschi* (Meglitsch 1967). Synapomorphies include the presence of the osphradium on the efferent membrane of the gill and the loss of the hypobranchial gland. The most unusual feature in this subclade is the knobs on the tentacles of *H. meglitschi* — evidently the parallel selection pressure toward gastropod structure in North America has turned it into somewhat of a pulmonate gastropod!

Two more paedomorphs, *Hamus russellhunteri* and *Hamus barcalolivorum*, are treated here as members of the Morton group. This placement is congruent with stratigraphic data and makes sense considering the academic parentage of their creators.

Several non-Anglo-American HAMs often superficially resemble or are erroneously attributed to insular *Hamus* species. For example, the South American HAM (Camacho 1966) resembles both *Hamus mortoni* and *Hamus mortonyongorum*. However, this similarity is entirely due to convergence. Camacho's HAM was copied with virtually no changes from Portmann (1960: fig. 1470). This, in turn, was a modification of a figure by Naef (1924), which, however, represented the ancestral conchiferan, not the ancestral mollusc. Naef derived the molluscs from the annelids, and Portmann reduced the gills from two pairs to one. There is also Dechaseaux's (1952) HAM species, which claims its ancestry as "after Lankester," but is in fact identical to the paleo-paedomorph *H. swinnertoni*.

## DISCUSSION

A major feature in Hammian evolution has been the expansion and enlargement of the posterior mantle cavity and the migration of gills into it (Fig. 10). It is significant that the posterior mantle cavity, with its paired gills and associated structures and orifices, is not an ancestral, but a derived condition. The canalization of HAM morphology also deserves special mention. In spite of new discoveries in the field of malacology, such as the discovery of living Monoplacophora in the 1950s or the recognition of the Rostroconchia in the late 1970s, the general morphology of *Hamus* species has remained little modified. Lineages that respond to changes in the environment tend to be short-lived and quickly go extinct. This phenomenon is particularly well documented in the



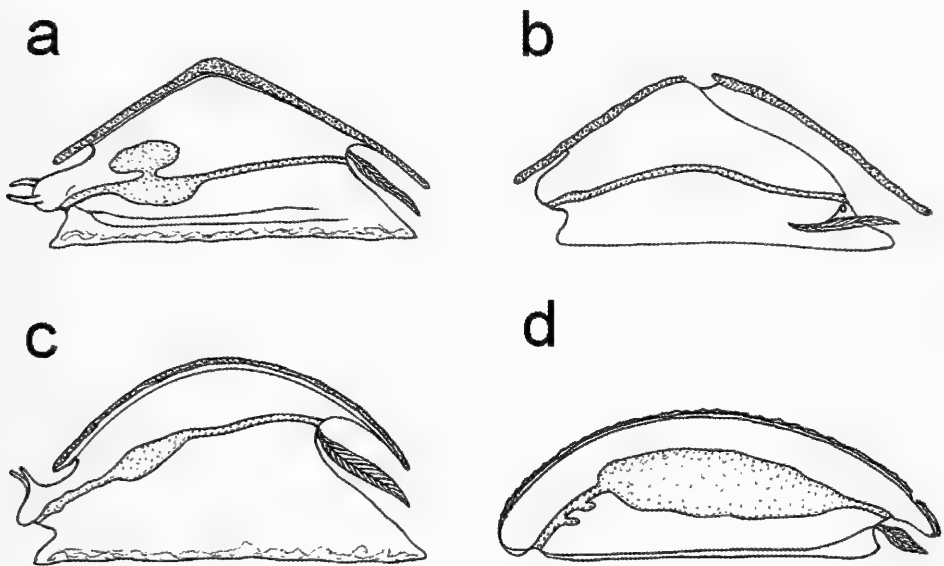


FIGURE 9. Paedomorphic and flatworm-like *Hamus* species. Paedomorphs include a. *H. swinnertoni*, b. *H. eastoni*, c. *H. russellhunteri*, and the flatworm-like d. *H. ravenjohnsonorum*. Note virtual lack of mesodermal structures (e.g., kidneys, heart, gonads). Redrawn from Swinnerton (1923), Easton (1960), Russell-Hunter (1968), and Raven and Johnson (1992), respectively.

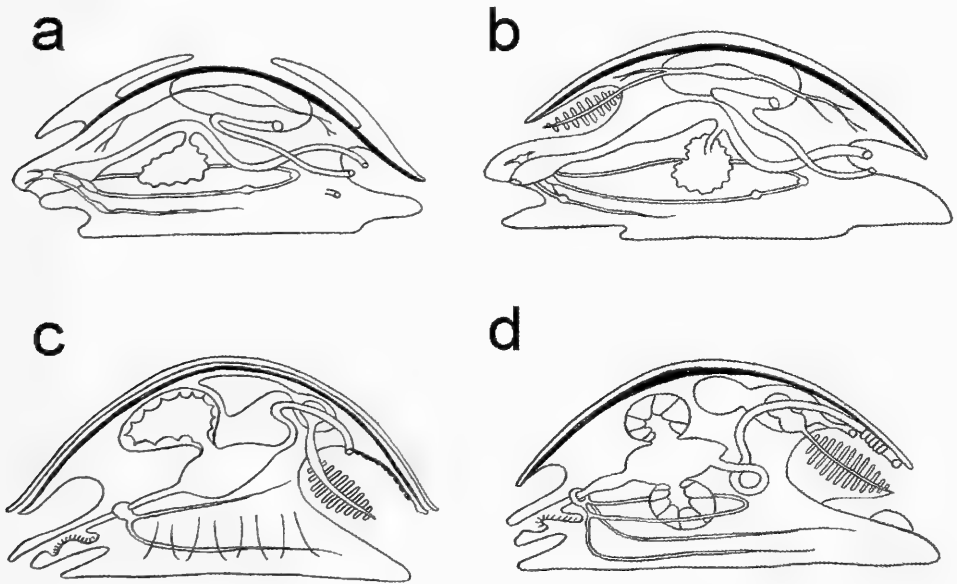


FIGURE 10. Generalized HAMs showing major trends in Hammian evolution over the last 150 years. Note increasing complexity and number of organs in transition from a→d, and the teratological *Hamus nicholsoni* (b) with its anterior mantle cavity, and yet untorted nervous system and alimentary tract. a. after Lankester (1883), b. after Nicholson and Lydekker (1889), c. after Barnes (1963), and d. after Seed (1983) (from Hickman and Lindberg 1985).

Morton lineage by *Hamus mortonyongorum*, *Hamus barnesi*, and *Hamus yongethompsonorum*. All three of these species have serial pedal muscles, reflecting the discovery of the monoplacophoran *Neopilina*. However, not one species that has originated since 1976 shows any segmentation whatsoever and only *H. barnesi* remains extant. HAM's normal environment is a sort of pedagogical refugium, in which degenerative reversions are quite common. Strong stabilizing selection may also have helped to keep HAM on a maladaptive peak.

The Morton group is convergent with the Gastropoda in many aspects of its anatomy. One wonders if some kind of mimicry is perhaps involved, though something more like lateral gene transfer is perhaps a better way to put it. Neontological and paleontological HAMs are interspersed throughout the early history of the group and have no intrinsic characters that distinguish them.

The evolution of HAM exhibits all the typical processes and developmental heterochronies thought to encompass organic morphological evolution, and therefore both phenetic and cladistic analyses have problems with pedomorphic taxa. Loss of organs and other features, particularly the radula and gonads, is a major process in HAM evolution (there are no data on how HAMs that lack gonads reproduce, but for modern species photocopying is a distinct possibility). Metamerism, or the duplication of structures, occurs in the pedal musculature, gills, digestive glands, and is — surprisingly — a derived rather than ancestral feature within the group. In many *Hamus* species, organs appear in the juvenile condition, although the animal as a whole is represented as an adult. Such pedomorphosis is seen in the various degrees of development of the nervous system. Loss of the gonads is perhaps a case of progenesis, these being the last mesodermal structures formed, but it is hard to see how such a change could not be a "lethal" mutation in terms of Darwinian fitness. The most extreme form of heterochrony in *Hamus* species appears in *Hamus swinnertoni*, *Hamus eastoni*, and *Hamus russellhunteri*. In these species only endoderm- and ectoderm-derived structures are present. Mesoderm derivatives fail to develop, and the degenerative anatomy of these species is readily apparent (Fig. 9).

### THE INFLUENCE OF HAM ON MOLLUSCAN STUDIES

HAM's fitness depends upon a symbiotic relationship with its pedagogical environment. It has not aided evolutionary biologists in solving problems, but it has often had the opposite effect, by requiring that theories be treated in the context of HAM. HAM has functioned as a Procrustean bed in molluscan phylogenetics because its advocates have presupposed as an answer what ought to have been the question. Namely, they have taken a phylogenetic hypothesis to be a fact, instead of testing its merit relative to some alternative. With the advent and implementation of molecular techniques over the last 10 years, many of the questions that HAM was inappropriately used to address have diminished in their import. Here we examine two previous uses of HAM in evolutionary debate — (1) determination of the sister taxa of the Mollusca, and (2) the anatomy and classification of Cambrian univalve molluscs. While the question of the sister taxon has moved from the morphological to the molecular arena, HAM's presence in the paleontological literature remains problematic. And regardless of the state-of-our-knowledge, both examples provide valuable insights into the risks associated with hypothetical ancestors and their uncritical 'evolution' as described above.

**FLATWORMS OR ANNELIDS?**—Prior to molecular data there were two major competing hypotheses about molluscan origins: (1) molluscs are modified flatworms, (2) molluscs are modified annelids. Ghiselin (1988) and Winnepeninckx et al. (1994, 1995) provide some of the earliest analyses of small subunit ribosomal DNA (18S) to address this question. These studies, and others, including Field et al. (1988), Lake (1990), Turbeville et al. (1991, 1992), have served as the

basis for many molluscan sister taxon comparisons, and they have consistently placed the Mollusca among the lophotrochozoan taxa (molluscs, annelids, brachiopods, bryozoans, and phoronids). However, the relative branching pattern for these taxa has yet to be resolved (Halanych et al. 1995). For example, Zrzavy (1998), using a combined analysis of 18S data and morphology, suggested that the sipunculids were the sister taxon of the molluscs. However, Boore and Staton (2002), using partial mitochondrial gene order data, suggested the sipunculids are actually more closely related to annelids rather than molluscs. Mallat and Winchell (2001), based on a 28S data set, suggested that brachiopods and/or phoronids may be the molluscan sister group. In no case have the flatworms been supported as the sister taxa of the Mollusca, so why was the prior debate so persistent? Was the morphological data so homoplastic and perplexing that previous workers were unable to resolve relationships?

In making phylogenetic statements based on morphology (or molecules) one should proceed as follows, compare the organisms, homologize as fully as possible, and treat the organisms sharing the most synapomorphies as sister-groups. One might also want to use additional techniques, but most people agree that we should at least do these things. If we do, it is clear that molluscs and flatworms share many symplesiomorphies — *e.g.*, spiral cleavage — which annelids also possess. But molluscs and annelids also share many synapomorphies not present in flatworms — an anus, a coelom, a particular larval type, just to mention a few. On this evidence, one has to conclude that the molluscs share a more recent common ancestor with annelids than they do with flatworms. To refute this line of reasoning, one must show that there are flatworm-mollusc synapomorphies not shared with annelids. Historically, the only ones worth mentioning are some alleged features of the pedal musculature, and hermaphroditism — the former evidently convergent and the latter demonstrably so. Alternatively, one has to disestablish the mollusc-annelid synapomorphies.

These arguments were readily available decades before molecular data, but because the flatworm theory and its implications, including the unsegmented HAM, had been presupposed, the annelid theory was widely dismissed. The arguments brought in to bolster an unsegmented HAM and the flatworm theory have been a veritable museum of fallacious logic. We give eight examples.

(1) We have the logical fallacy of basing an argument upon negative evidence. Lack of evidence that X occurred is taken as evidence that Y occurred. We are told that annelidan conditions are not recapitulated, as in certain aspects of the development of *Chiton* (Hammersten and Runnström 1925). There are plenty of examples of non-recapitulation, for instance chicken-teeth. When something is recapitulated, it is a fact to be explained, and nothing more.

(2) We have the formal fallacy of irrelevant conclusion. Russell-Hunter and Brown (1965) assert that *Neopilina*'s structure does not fit Hyman's definition of "metamerism." The question is not whether how somebody uses a word applies, but rather what has happened. The issue is not whether molluscs "are" segmented, but what their ancestors were, and what their relationships are.

(3) We have rampant *ad hoc* hypothesizing. Many authors have been able to imagine reasons why, say, *Nautilus* needs more gills (Hoffmann 1937), but they need additional *ad hoc* hypotheses to explain away the multiple kidneys, and coelomoducts.

(4) We find a habit of treating the relational property "primitive" as if it were, like "spiny," an intrinsic one, to be read off without comparison. Korschelt and Heider (1900) argue, in so many words, as follows: Cephalopods are advanced; *Nautilus* is a cephalopod; *Nautilus* has four gills; therefore, having four gills is an advanced trait. It is curious that among the cephalopods *Nautilus* is considered "primitive" — except in precisely those features in which it contradicts HAM and the flatworm theory.

(5) We get a conflation of historical relationships and what we see in extant forms. Clark (1980) claimed to have discovered the perfect example of metamerism in oligochaetous annelids.

Molluscs, he said, are different, and therefore are not derived from annelids. This amounts to belief in a physiological essence. Segmentation, like all sorts of other things, has evolved. There is no reason to believe that the physiologically ideal state represents the ancestral one, and even if it did, it would not show a lack of descent.

(6) We find the *possibility* of an event having occurred treated as if it *had in fact* occurred. Clark, again, shows that metamerism has evolved independently among tapeworms, chordates, and the annelid stock. If not three times, why not any number at all? The opposite conclusion accords with the principles without which it is impossible to infer relationships at all.

(7) We have circular reasoning, or begging the question, in which attempts to support the flatworm model presuppose that the flatworm theory is true. Particularly in the works of Stasek (1972), we find it asserted that molluscs are “pseudometamerous.” Why not “vestigially metamerous?”

(8) And, finally, we have an abuse of scenarios. There is some healthy controversy as to what role scenarios ought to play in phylogenetic research. But if one is to use them, one ought to do so logically. A logically legitimate role that they can play is in testing hypotheses. If a theory implies the existence of hypothetical organisms that would not have been viable, that theory is false. But it is the logical fallacy of denying the antecedent in a conditional statement, to “confirm” hypotheses by showing that they do not contradict particular theses. Thus, both Stasek (1972) and Salvini-Plawen (1980) provide us with a long account of what happened physiologically as flatworms were transformed into molluscs — never considering the obvious fact that the annelid theory can accomplish the same end, without the long list of imaginary intermediates and numerous convergences that the flatworm theory and HAM demand.

Of course, there is no real evidence that HAM ever existed. Indeed, the non-conchiferan molluscs (aplacophorans and chitons) have been treated as “non-molluscs” by some authors because they lack the “defining characters” found in HAM (e.g., Odhner 1919), and the lack of an HAM stage in the ontogeny of any extant mollusc was first noted by Verrill (1896).

Today, the “flatworm versus annelid” controversy is being argued in somewhat different terms. Some authors argue that body ‘segmentation,’ upon which the supposed relationship of the molluscs, annelids, and arthropods was largely based, is actually convergent. In parallel, our understanding of fine structure, development, and “segmentation” of both molluscs and annelids has also markedly increased with the application of modern imaging and developmental techniques as well as detailed anatomical studies of basal molluscan groups (e.g., Salvini-Plawen and Bartolomaeus 1995; Haszprunar and Schaefer 1997; Wanninger and Haszprunar 2002). Others, however, maintain very much the opposite thesis, namely that segmentation has been secondarily reduced not only in molluscs but in many other groups and may even go back as far as the bilaterian common ancestor (Balavoine and Adoutte 2003). Part of the evidence comes from molecular trees, which show that some animals with no obvious trace of segmentation are closely related to those with it. In some of these, such as echiurans, there are morphological traces of segmentation as well (Hessling 2002). The mechanisms that control the morphogenesis of segments in all animals have been widely homologized as well. There may, however, have been a considerable amount of parallelism involved, so that the seriality was not as widely expressed as it is, for example, in modern arthropods and annelids. At the very least, given that molluscs and annelids are more closely related to each other than to arthropods, the kind of segmentation that has been hypothesized to have been present in the common ancestor of annelids and arthropods must either be convergent or have been secondarily reduced in Lophotrochozoa. Two theoretical points are worth mentioning in this connection. In the first place, the notion that evolution always proceeds from simple to complex was very common in the nineteenth century, and it is about time that it no longer be presupposed in efforts at phylogenetic reconstruction. Second, there are good theoretical reasons for thinking

that it is easier for parts to be lost than gained. Our views on such matters may profoundly affect our conclusions, but they are rarely made explicit. Although the ultimate outcome of the "segmented common ancestor" question for the Mollusca remains elusive, we need to proceed with care and rigor in testing alternative hypotheses and not rely on imaginary creatures to parse and test data as in the past.

**USE AND ABUSE OF FOSSIL HAMS.**—Paleontologists often try to stuff HAM into shells as if they were dishing out escargot. Following a tradition that goes back at least as far as Knight (1952), Peel (1974, 1991) and others have loaded large bellerophon shells onto tiny HAMS. The alternative that at least some bellerophon shells were slugs was well argued by McLean (1984). Others, such as Knight (1952), Pojeta and Runnegar (1976), and Peel (1990, 1991), tested alternative morphologies (*i.e.*, torted or non-torted) for extinct Paleozoic molluscs, based on the fit of fossil conchs, resplendent with holes, tubes, slits, and trails, on HAM's anatomical body plan. Here we have real data being "tested" against a hypothetical anatomy to determine whether the hypothesis shall be accepted or rejected on the grounds of which reconstruction "looks comfortable." Paleontologists may claim to base their inferences on the fossil record and the structure of extant organisms. But in the case of molluscs, their procedure all too often has been to use an imaginary organism — HAM — as a Procrustean bed, to which the soft parts of fossils are fitted by adding features here, lopping off others there, and stretching the data wherever they fall short of the desired effect.

Because of the use of HAM to distinguish untorted molluscs from torted gastropods, it has surreptitiously become a linchpin in some torsion scenarios. Ghiselin (1966) suggested a possible scenario for the non-saltatory origins of gastropod torsion. Batten, Rollins and Gould (1967) countered with claims based upon unpublished results. These results, subsequently published by Rollins and Batten (1968), employed HAM to justify the non-torted nature of the mollusc used to argue against Ghiselin's scenario. And, although Harper and Rollins (1982) ultimately retracted their claims, the damage had already been done, and this episode has been used to discredit functional thinking.

Sanitation issues are often evoked in torsion scenarios because many of the holes, tubes, slits, and trails of the fossil conchs are frequently linked with hypothetical water circulation patterns in the HAM anatomy so that waste products will be removed from the mantle cavity. It is interesting to note that Pelseneer (1894), who first discussed the sanitation problems that molluscs face with the anus and gills in close proximity, also was the first to pen a HAM with the gills located *within* the mantle cavity! Sanitation problems for *Hamus* species were intensified in 1952 when a new character state appeared in the common ancestor of *Hamus moolafisherorum* and the Morton/Easton groups (Fig. 5). This synapomorphy was the placement of the anus **above** the gills rather than below them (*i.e.*, downstream) (Appendix, character 20); so much for intelligent design. Although potential outgroups such as chitons and monoplacophorans have the anus and gills separate and the anus located below the gills, *Hamus* evolution has not converged with these functioning anatomies and, instead, has been directed towards an ever increasingly maladaptive state. Because of its more problematic nature, these maladaptive characters in the HAM phylogeny provide a much larger arena for speculation and interpretation and are vastly more interesting than the character states found in real organisms.

## SUMMARY

The difficulties associated with reconstructing relationships, hypothetical taxonomic units, fossil anatomies, and incorporating fossil taxa into evolutionary scenarios by no means implies that we should give up. Rather, we should try alternatives, especially alternatives to HAM. Many of our colleagues have argued that HAM should be allowed to exist as a sort of pedagogical fairy tale, justified as a means of teaching molluscan anatomy. They acknowledge that no such creature ever

existed and that any evolutionary scenario deriving molluscan taxa from it represents misinformation. Such arguments remind us of ones given in favor of paraphyletic taxa. Unfortunately, neither the imaginary animals nor the misleading groups come clearly labeled with warnings about the harm that they might do if mistaken for real organisms or monophyletic units.

It is our conclusion that HAM is a pest being preserved in a textbook refugium, and science needs a better basis for determining the structure, relationships, and classification of organisms than an expedient of didactics and pedagogy. The sooner all *Hamus* species become extinct the better.

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Appendix

DATA MATRIX FOR *HAMUS* SPECIES

Taxon	Character Number			
	000000000	111111111	222222222	3333333
	123456789	0123456789	0123456789	0123456
<i>H. huxleyi</i>	?0?000000	00000000?0	0000?00000	0?00000
<i>H. lankesteri</i>	010010000	0111000002	0021000010	0?11100
<i>H. nicholsoni</i>	111000110	0111000002	0030?01110	0?11100
<i>H. pelseeneeri</i>	111010100	01100001?2	0011101110	0?21100
<i>H. swinnertoni</i>	111010100	0111000012	02?0?01110	0?14011
<i>H. borrapottsorum</i>	111010100	0111000012	0021100110	0?21100
<i>H. moolafisherorum</i>	111010100	0111000002	1110?01110	0?24000
<i>H. mortoni</i>	111010100	1010110021	1011110121	1024100
<i>H. eastoni</i>	110010100	01110001?2	12?0?01110	0?14011
<i>H. barnesi</i>	111111101	1110001011	1021101110	1124100
<i>H. mortonyongorum</i>	111110100	0110000011	1011110111	0?24100
<i>H. hickmani</i>	111010100	1110001012	1021100111	1014100
<i>H. meglitschi</i>	111010100	1111101012	1021100110	1124100
<i>H. russellhunteri</i>	111010100	01110001?2	12?0?01110	0??4011
<i>H. staseki</i>	111111000	01100001?2	00110?1110	0?1410?
<i>H. yongethompsonorum</i>	111110100	1110100011	1011110111	1124100
<i>H. barthbrosonorum</i>	111010100	0110001012	1021100111	1021100
<i>H. bossi</i>	?2?110100	01100001?2	1021001110	1222100
<i>H. seedi</i>	111010101	1100001021	1011001111	1024100
<i>H. barcalolivorum</i>	111010100	0110000011	1011100110	0?23100
<i>H. ravenjohnsonorum</i>	?2??10100	01100001?2	12?0??1110	0?24011
<i>H. salvinisteinerorum</i>	?2?110100	01100001?2	1011101110	1224011
"Cambrian" taxa				
<i>H. pojetarunnegarorum</i> species complex:				
Taxon a	111010110	01110001?2	0210??0110	0?24011
Taxon b	111010120	01110001?2	0210??0110	0?24011
Taxon c	110010110	01110001?2	0210??0110	0?24011
Taxon d	110010120	01110001?2	0210??0110	0?24011
Taxon e	110010110	01110001?2	1210??0110	0?24011
Taxon f	110010120	01110001?2	1210??1110	0?24011

## CHARACTER ANALYSIS

**Integument**

1. Shell enveloped by mantle. The plesiomorphic state is equivocal as the outgroup lacks a shell. States — shell enveloped by mantle = 0, shell not enveloped by mantle = 1.
2. Exoskeleton. Shell absent is the plesiomorphic state. States — shell absent = 0, shell present = 1, integument with spicules = 2.
3. Shell with opening. The presence of an opening in the shell is equivocal. States — shell opening present = 0, shell without openings = 1.
4. Shell attachment muscles. The absence of multiple muscles is plesiomorphic. States — multiple muscles absent = 0, multiple muscles present = 1.

**Foot**

5. Foot divided into propodium, mesopodium and metapodium = 0, foot not differentiated = 1.

**Gills**

6. Number of gills. A single pair of gills is plesiomorphic. States — single pair of gills = 0, multiple gills = 1.
7. Gills enclosed in a mantle cavity (internal) or extending beyond body (external). External gills are plesiomorphic. States — external gills = 0, internal gills = 1.
8. Gill position on body. Gills situated on the posterior portion of the body are plesiomorphic. States — posterior placement of gills = 0, anterior placement of gills = 1, lateral placement of gills = 2.
9. Efferent membrane. The absence of an efferent membrane from the gill to the roof of the mantle cavity is plesiomorphic. States — gill without efferent membrane = 0, gill with efferent membrane = 1.
10. Afferent membrane. The absence of an afferent membrane from the gill to the floor of the mantle cavity is plesiomorphic. States — gill without afferent membrane = 0, gill with afferent membrane = 1.

**Digestive System**

11. Jaws. The presence of jaws in the buccal cavity is plesiomorphic. States — jaws present = 0, jaws absent = 1.
12. Buccal mass. The presence of a buccal mass is plesiomorphic. States — buccal mass present = 0, buccal mass absent = 1.
13. Radula present in oral cavity. The presence of a radula is plesiomorphic. States — radula present = 0, radula absent = 1.
14. Salivary glands. The absence of salivary glands is plesiomorphic. States — salivary glands absent = 0, salivary glands present = 1.
15. Esophageal glands. The absence of esophageal glands is plesiomorphic. States — esophageal glands absent = 0, esophageal glands present = 1.
16. Configuration of intestinal tract. A straight, non-looped intestinal tract is plesiomorphic. States — intestinal tract straight = 0, intestinal tract looped = 1.
17. Digestive gland. The presence of a digestive gland is plesiomorphic. States — digestive gland present = 0, digestive gland absent = 1.
18. Position of digestive gland relative to the stomach. A ventral digestive gland is plesiomorphic. States — digestive gland ventral = 0, digestive gland dorsal = 1, both dorsal and ventral digestive glands = 2.
19. Style. The presence of a style sac without a style is plesiomorphic. States — sac without style present = 0, style present in stomach = 1, both sac and style absent = 2.
20. Anus position. An anus opening below the gill is primitive. States — anus positioned below the gill = 0, anus positioned above the gill = 1.

### **Coleomic structures**

21. Heart and pericardium. The presence of a heart is plesiomorphic. States — heart present = 0, heart and pericardium present = 1, heart absent = 2.
22. Aorta. The presence of an anterior aortic branch is plesiomorphic. States — anterior aorta only = 0, aorta absent = 1, anterior and posterior aorta = 2, posterior aorta only = 3.
23. Gonads. The absence of gonads is plesiomorphic. States — gonads absent = 0, gonads present = 1.
24. Gonoducts. Separate gonoducts are plesiomorphic. States — separate gonoducts = 0, gonads opening into pericardium = 1.
25. Kidney morphology. Tubular kidneys are plesiomorphic. States — kidneys tubular = 0, kidneys spherical = 1.

### **Sensory structures**

26. Cephalic tentacles. The presence of cephalic tentacles is plesiomorphic. States — cephalic tentacles present = 0, cephalic tentacles absent = 1.
27. Statocysts. The presence of statocysts is plesiomorphic. States — statocysts present = 0, statocysts absent = 1.
28. Epipodium and tentacles. The presence of an epipodium without tentacles is plesiomorphic. States — epipodium present = 0, epipodium absent = 1, epipodial tentacles present = 2.
29. Hypobranchial gland. The absence of a hypobranchial gland is plesiomorphic. States — hypobranchial gland absent = 0, hypobranchial gland present = 1.
30. Osphradium. The absence of an osphradium is plesiomorphic. States — osphradium absent = 0, osphradium present = 1.
31. Osphradium position. The position of an osphradium on dorsal surface of foot is plesiomorphic. States — osphradium on dorsal surface of foot = 0, osphradium present on efferent membrane = 1, osphradium present on dorsal surface of pallial cavity = 2.
32. Eyes. The presence of stalked eyes is plesiomorphic. States — stalked eyes = 0, non-stalked eyes = 1, eyes absent = 2.

### **Nervous system**

33. Ganglia. The presence of four pairs of ganglia (cerebral, pedal, parietal, buccal) is plesiomorphic. States — all four pairs of ganglia present = 0, three pairs present (cerebral, pedal, parietal) = 1, cerebral only = 2, cerebral + pedal = 3, ganglia absent = 4.
34. Pedal nerve. The absence of pedal nerve cords is plesiomorphic. States — pedal nerve absent cords = 0, pedal nerve cords present = 1.
35. Visceral nerve loop. The presence of a visceral nerve loop is plesiomorphic. States — visceral nerve loop present = 0, visceral nerve loop absent = 1.
36. Nerve ring. The presence of a nerve ring around the pharynx is plesiomorphic. States — nerve ring around the pharynx = 0, absence of nerve ring around the pharynx = 1.

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*Alan E. Leviton, Ph.D., Editor*  
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